From stimulus to response: Analyses of electrophysiological and behavioral indicators of sensorimotor interaction processes in linear movements to kinesthetically and visually defined spatial locations

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Waldemar Kirsch
aus Kairakkum

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Erstgutachter.....Prof. Dr. Frank Rösler
Zweitgutachter.....Prof. Dr. Karl R. Gegenfurtner
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1 Preface

1.1 Theoretical and empirical background

Reaching out for and grasping objects belongs to our daily behavior. Given the effortlessness of these motor acts one may be surprised at the huge complexity and plurality of processes taking place between sensory input and motor output. A simple reaching movement for a cup of coffee implies several processing steps from the sensing initial hand and target positions to the transformations of this information into patterns of muscle activity among others.
Much attempt was made within several research areas to describe possible functional and neuronal mechanisms underlying these processes. One of the essential questions relating to functional aspects proved to be related to the level of processing at which relevant stimulus information is maintained and used for motor planning.
It is a common experience that even in the absence of vision we are able to identify a spatial location of an object after a movement, move away from it, and then point back to that same position. For instance, while reading a newspaper we may put a cup of coffee on a desktop without seeing it and reach for it again after a delay. What kind of representation does the brain maintain and use for planning a movement in similar situations? Within a research domain, which aims to answer these kinds of questions, several information sources are discussed. Some findings suggest that the subjects rather code a static target location within a spatial frame of reference (e.g. Baud-Bovy & Viviani, 1998). Others argue for rather "intrinsic" sources, like final posture (e.g. Rosenbaum, Meulenbroek, & Vaughan, 1999) or dynamic movement information (e.g. Millar, 1994) as possible basis for motor planning in kinesthetic matching tasks. There is neither a theoretical nor an empirical basis up to now that can explain the obtained discrepancies of the results.
The current state of research in the visuomotor area is more complex, but similar. A series of psychophysical studies indicated a rather serial course of computations from the retinocentric target coordinates to body centered planning (e.g. Flanders, Tillery, & Soechting, 1992). According to this, the initial target representation is assumed to be transformed in head-centered coordinates by comparing retinal signals with an internal representation of eye position. Then, head-position signals are combined with a head-centered target representation providing body-centered target coordinates. Finally, movement kinematics are derived from comparing target and joint positions, which are represented in the same frame of reference at this processing stage. On the other hand, based on evidence from single cell recordings a

rather direct transformation schema was suggested (e.g. Buneo, Jarvis, Batista, & Andersen, 2002). Within this model the current target and hand positions are integrated on the level of eye coordinates. Both planning modes were supported by several findings and some extensions and modifications were suggested. Considering as a whole, the results indicate a complex and ambiguous picture, in which the involvement of a specific mechanism seems to be task and context dependent (e.g. Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003). Despite the complexity of sensorimotor processes and possible methodical deviations, like the use of dependent measures and experimental designs, what could be the reason for contradictory results suggesting rather different scenarios for similar task situations?

One potential aspect that might possibly help to resolve some discrepancies stems from a further line of research focusing on sensorimotor interactions.

Our introspective thinking is affected by the view that perceptual processes (i.e. conscious identification of locations and identity of environmental objects) precede our motor behavior. This assumption, which was already argued by Descartes (see e.g. Rossetti, 1998), is not more exclusively supported by research. A series of impressive findings in brain-damaged patients demonstrated that despite deficits in perception of objects characteristics, like their orientation or location, the patients were able to use sensory information to guide their motor behavior and contrariwise, to perceive objects being unable to correctly perform sensory guided movements (e.g. Goodale & Milner,1992, Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999, Paillard, 2005, Paillard, Michel, & Stelmach, 1983, Rossetti, 1998). Based on these and on a considerable number of other results from several research areas, two distinct modes of sensorimotor processing were proposed. Absolute metrics of an object, which are primarily relevant for a motor response are assumed to be processed within a direct system, labeled as “pragmatic” (e.g. Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), “sensorimotor” (e.g. Paillard, 1987) or “how/vision-for-action” (e.g. Goodale & Milner,1992). On the contrary, a “cognitive” mode (also labeled as “semantic”, “representational”, “vision-for-perception”) enables to create an internal representation by binding stimulus attributes as well as by computing relational metrics of the environmental events. In addition to the functional dissociation (motor behavior vs. perception), several other dichotomies relating to sensitivity, neuronal substrate, speed or consciousness were proposed (e.g. Norman, 2002). One critical aspect among these seems to be the time between stimulus and response (e.g. Rossetti & Pisella, 2002, Goodale, Westwood, & Milner, 2004). The direct system is assumed to operate in “real-time” (i.e. “here and now”) and thus, to provide a rich and detailed actual representation of an object and its position in respect to the observer and / or to the effector

that is used for action (i.e. egocentric metrics). In contrast, the "cognitive" mechanisms operate at a longer time scale, being however dependent on less exact metrics (relational) due to signal reduction processes (e.g. Rossetti, 2003, Goodale et al., 2004).

Despite similarities relating experimental conditions implemented within three mentioned research domains, the results are usually interpreted within distinct conceptual schemas (e.g. in terms of different processing modes vs. in terms of information sources used for planning). Although a direct link between the two proposed processing modes and the planning assumptions may not be compelling, due to a different emphasis of certain aspects of spatial processing among others (e.g. egocentric vs. allocentric, eye centered vs. body-centered representations) they may be linked to each other on a more abstract conceptual level. According to Rossetti (2003) the dual-system approaches can be related to the classical reflex-voluntary oppositions and have several counterparts within scientific literature. Thus, if a direct "sensorimotor" system may be associated with a type of "low-level" representations for sensorimotor transformations (e.g. Jeannerod & Jacob, 2005), then not only allocentric mapping, but also any "spatial" mechanisms may not be necessary (see e.g. Berthoz, 1991 for a model of generation orienting movements suggesting a direct sensorimotor coupling without any spatial reconstruction processes). Evidence for such direct loops are reported for instance, within the saccadic movement research (e.g. Berthoz, 1991, Stein, 1991, Colby & Goldberg, 1999). In this research area two alternative mechanisms are discussed. According to one of them, the oculomotor system access to the position of the target in head-centered coordinates (i.e. to a "spatial" target representation). The other is assumed to operate on the level of the retinal target coordinates and seems to be better supported by the research as the prior (i.e. retinocentric information is directly used for generation of motor program without any "real-space" representations). Interestingly, Jacques Paillard, who strongly influenced the "dual-mode research", used this dissociation among others as evidence for the distinct sensorimotor modes ("sensorimotor" vs. "representational") for eye movements, but not for hand movements, where mainly the egocentric-allocentric dimension was applied (Paillard, 1987). More recently (2005), he also argued for a dissociation between "internal" and "external" loops within the somatosensory system ("visually configurated body image" vs. "proprioceptively framed body schema") emphasizing however again a configural vs. body-centered distinction for "body image" and "body schema" respectively (although intrinsic vs. spatial dimension would also be appropriate).

Following these results and assumptions, one may suggest that the findings reported by Buneo et al. (2002) and indicating a rather direct planning using for visuomotor behavior may be

attributed to a direct “sensorimotor” mode in the sense of the dual-system approaches due to a lack of spatial representations. In contrast, a serial course of processing including the computing of spatial coordinates, as suggested by Flanders and colleagues (1992), may rather reflect a more “abstract” coding of sensory information and consequently a “representational” processing mode. Similarly, using kinesthetic sources, like dynamic movement or posture information for planning in the absence of vision may be associated with a rather direct type of processing (“sensorimotor”) since computations occur within the intrapersonal space (this type is also discussed as “direct mapping hypothesis”, see e.g. Baud-Bovy & Viviani, 1998). On the contrary, if a target location in a spatial frame of reference is extracted based on internal signals, one may argue that this would rather be related to “an internal representation of the environmental space” (Paillard, 1987) und thus to a “representational” processing mode (see also “target position hypothesis”, Baud-Bovy & Viviani, 1998). This view seems to fit rather well into the core concept of the two proposed processing modes suggested by Paillard (e.g. 1987):

> “…The first refers to a sensorimotor mode of processing spatial information. It mainly concerns that part of the physical world to which each organism is attuned by virtue of its basic sensorimotor apparatus. It entertains a direct dialog with that world and thus contributes to the continuous updating of a body-centered mapping of extracorporal space where objects are located and to which action is directed.
>
> The second results from a representational mode of processing spatial information. It derives from neural activities that explore and consult mental representations of the physical reality that are embodied in memory stores. It allows neural processing to step back from the immediate sensory input and to become progressively free from the environmental constrains under which sensorimotor analyzers have to work…”

Although rather speculative, the assumed link between the “dual-system” and “planning” models seems to be not implausible. It is widely accepted that the CNS is an “optimized” system which selects the most economical solution to perform a given task. In this context, the direct planning schemata may be expected to be more efficient as others using additional transformations (e.g. Desmurget, Pelisson, Rossetti, & Prablanc, 1998, Andersen & Buneo, 2002). However, if the time between stimulus and response is taken into consideration, such direct mechanisms may not be appropriate, since they are directly coupled with the actual sensoritopic object and effector information. For instance, a new sensory input arriving after a target in the same modality may interfere with it. Thus, some “more stable” informational formats may have advantages over sensoritopic representations, when information has to be retained over time. This idea seems to be partly supported by a simple analysis of time delays between stimuli and responses implemented by the studies (see manuscripts).

In summary, if the two-system approaches and the link between them and the mentioned planning schemata are appropriate, then the core difference between “sensorimotor” and “representational” mechanisms may be associated with *internal* vs. *extracorporal* sensorimotor loops, which may be involved differently dependent on the time of response in both, kinesthetic and visual modality. This may possibly explain some diversity of the empirical results and derived hypotheses within both areas to some extent.
Based on the outlined theoretical and empirical basis and starting from the assumption that the time between stimulus and response may affect the involved mechanisms, we conducted a series of behavioral and EEG experiments, in which we investigated the role of stimulus-response delays in sensorimotor processes in the kinesthetic and the visual modality. The main question of interest behind all of the used experimental designs was: whether time-dependent changes of processing characteristics are observable and how they may be related to the empirical and theoretical findings mentioned above.

1.2 Goals and outcomes of the performed experiments

In the first two behavioral experiments we tested the effects of verbal-cognitive and motor interfering activity on the retention of relevant information in a motor matching task. For this purpose we adopted the classic rationale of distractor experiments and assumed that if the same mechanism is involved independent from the delay duration, a similar influence of an interpolated task on reproduction may be expected.
The blindfolded subjects were asked to move a handle with their right hand until a stop and then back and to reproduce the given stop position by another movement. We adjusted the intervals between the two imperative Go-signals so that the reproduction tone occurred approximately 0 and 8 seconds after the first backward movement in both experiments (i.e. immediate reproduction was compared with delayed reproduction).
After the first backward movement a verbal judgment of the movement / target distance was required in one condition of the first experiment. In the control condition the retention interval was “unfilled”. Analyzing constant and variable errors, which reflect systematic over- or underestimation biases and response variability correspondingly, we obtained that the verbal judgments interfered with the motor reproduction only, when the retention interval was long. The variable error increased as compared with the control condition. Moreover, movement amplitude was widely unaffected by the reported distances.

Instead of verbal distance estimations we asked the subjects to perform an additional movement with their right or left hand during the retention interval in the second experiment. Except for a control condition, all other manipulations were the same. The type of the interpolated movement (right vs. left hand) proved to be important during both delay conditions. In the short delay condition the amplitude of reproduction movements was higher when the intermediate task was performed with the left hand as compared with the corresponding "right hand task". When the delay was long, an opposite effect was evident. Thus, the results of both experiments suggested that processing characteristics relating retention of kinesthetic information and / or motor planning may change dependent on the time of response. Moreover, they seemed to indicate that information used for planning of reproduction movements is rather *kinesthetic* and *dynamic* (i.e. computation occurred within an "interpersonal" space), when response is required immediately and rather *static* and *spatial* (i.e. access to rather "extrinsic" information sources), when a delay of several seconds is introduced.

Following this a further experiment was carried out, in which reproduction of terminal locations vs. movement distances was required. The goal of this study was to characterize the retention mechanisms of *static* ("location reproduction") and *dynamic* ("distance reproduction") information sources. Using a similar test arrangement as in the two previous experiments, we compared the performance in both reproduction conditions dependent on the delay interval that remained the same ("0" vs. "8" seconds). The subjects moved the right hand until the stop and back, being however stopped before they reached the initial start position. From this new point they had to move the handle as far as the first movement was (distance reproduction) or until the memorized stop position (location reproduction). The results indicated rather different characteristics of kinematic parameters of reproduction movements dependent of whether distances or locations were reproduced. During the distance reproduction, the subjects followed the rather untypical dynamic of the first movement as indicated by the corresponding acceleration profiles. In contrast, the kinematics of the movement reproduction phase in the location condition had usual characteristics obtained during unrestricted movements to visual targets. These results and an additional correlation analysis suggested that the distance condition was associated with the dominance of dynamic control variables, while static aspects prevailed, when the terminal location had to be reproduced. The analyses of reproduction errors revealed somewhat ambiguous results. On the one hand, we obtained a comparable response variability of both response mode conditions, when the delay was short. This result confirmed our prediction that dynamic and

static cues can reliably be used if a response is required immediately. On the other hand, an increase of variable error in the location reproduction condition was obtained, when the delay was long. No such delay dependent changes in the distance condition were present. This outcome seemed to suggest that dynamic movement information did not deteriorate over an empty interval, while static sources did. However, the results from this experiment allowed only restricted statements about the performance due to the implemented change of starting position and the type of dependent measures used.

In order to overcome these caveats, which make established conclusions difficult, we used a simple task by asking the subjects to reproduce the position of the stop and by varying the delay in milliseconds (Experiment 4) and in the seconds range (Experiment 5) in the last two behavioral experiments. We aimed to pursue the performance without any additional constraints. In addition to the error measures we also used maximal deceleration as the dependent variable, which proved to be important in dissociating the dynamic and static control aspects in the previous study. According to the prior results, the question of interest was: whether indices for time dependent changes of processing characteristics from dynamic to static aspects are detectible. In fact, similarly to the distance reproduction condition of the previous experiment we obtained the untypical deceleration strategies in the short delay conditions indicating the use of rather dynamic information sources and an obvious successive deviation from this pattern, when the delay was extended to more than one second. Moreover, a “range effect” indicating an influence of target-context was not detectible in the short delay conditions, but was evident in the range of seconds. Additionally, the constant and variable errors followed two different functions rather than one with monotonic course in both experiments potentially indicating two “temporal markers” or three different processing formats, which may be associated with the obtained changes of processing characteristics. This assumption was used as a starting point for the investigation of electrophysiological markers of sensorimotor processes in the kinesthetic domain (EEG-Study1). We expected a similar delay dependent modulation of bran activity if retention of information and motor planning occur within one functional system (e.g. rather “poor” amplitude differences across delay conditions without topographical changes would speak for “quantitative” differences). In contrast, if delay-dependent changes of generator configurations as expressed in different topographies in relevant processing epochs are observable, the functional mechanisms may be assumed to be distinct. The general task was the same, as in the last two experiments. The blindfolded subjects moved their right hand until they were stopped and then back and tried to reproduce the position of the stop by another movement. Three delay conditions were

implemented. The reproduction was required immediately, about one second and about five seconds after the first backward movement. In addition to measuring the movement parameters, we recorded EEG (electroencephalogram) data. The analyses of kinematic data revealed an additional support for the hypothesis that the immediate reproduction is rather associated with the use of dynamic control parameters, while reproduction after a delay of seconds rather relies on static control mechanisms. The EEG data was analyzed in respect of the evoked activity during defined processing epochs. Several methodical procedures were applied to the ERPs (Event-related potentials) aiming to investigate the differences across the delay and the distance conditions.

In respect to the delay manipulation, we identified voltage-amplitude modulations in many selected time-windows starting from the end of the first backward movement. One characteristic feature of these effects seemed to be composed of differences of hemispheric dominance. When the delay was short, negative activity over premotor and motor areas was stronger over the left than over the right hemisphere and contrariwise, stronger over the right that over the left hemisphere, when the delay was long. In the middle delay condition no pronounced laterality effects were obtained. This result confirmed a current hypothesis suggesting the role of the left hemisphere in the control of rather dynamic parameters and the involvement of the right hemisphere in the processing of rather static aspects of motor behavior. The ERPs of the delay phase seemed to suggest further that neuronal networks participating in the retention of kinesthetic information and / or motor preparation were distinct dependent on delay condition. Additionally, not only regional characteristics, but also functional properties of activation as expressed in polarity of the measured signal appeared to differ across three delays. These results can hardly be reconciled with only one uniform functional mechanism of information retention and motor planning used in all delay conditions. Instead they indicate changes in processing depending on the time of response and confirmed the results of the previous behavioral experiments.

Due to a high complexity of data especially arising from temporal overlapping of processing epochs and to a lack of comparable studies, this conclusion remains preliminary. In order to test the validity of the results and to reduce the data-complexity to some extent, another EEG-Study was conducted (EEG-Study 2). We asked the subjects to memorize spatial locations of visual stimuli (LEDs) arranged in the same way as the stop positions used previously. An imperative acoustic signal indicating reproduction movements to the memorized locations was presented 200, 1000 and 5000ms after the target offset. The performed kinematic and error analyses revealed distance and delay effects, which may theoretically be explained

within one-mechanism approach (e.g. as an increase in sensory noise within one functional system). However, the ERP results strongly suggested that motor planning relied on qualitatively distinct processes dependent on delay duration. Not only different dynamics of evoked activity were obtained, but also distance effects occurred at different sites dependent on delay condition.

Moreover, a distance specific modulation of a series of ERP components shortly before and during movement execution phases in both EEG studies was obtained. These results indicated a type of “mental chronometry” of movement programming and control processes in response to kinesthetic and visual targets. The temporal and regional properties of these activation patterns were attributes to possible functional aspects, like to sensory and internal feedback mechanisms discussed in the motor research literature. The most pronounced distance effects observed at the end of movement execution were associated with a modulation of a negative deflection over primary motor areas, which seemed to be strongly related to on-line adjustments of movement trajectory. These results as a whole and the last finding in particular, bear direct reference to basic questions of motor processes, like “planning vs. control”, “open-loop vs. closed-loop”, “continuous vs. terminal control of movement trajectory” and provide an opportunity to investigate these rather directly.

In summary, although some conclusions may not be compelling and have to be validated by further research, the bulk of evidence rather confirms several distinct sensorimotor mechanisms, which may be involved dependent of a stimulus-response delay. Moreover, in the case of the kinesthetic modality information processing seemed to “remain” within an intrapersonal space, when an immediate response is performed. I.e. the subjects rather tended to reproduce the first movement than to extract a spatial location of the target in these conditions. Conversely, they rather used a static and probably extrinsic target representation for motor planning, when delay was extended to several seconds. At this point our results do not seem to contradict neither the dual-system assumptions nor planning schemata mentioned above. One may argue that intrinsic computations are rather direct and occur within “the proprioceptive field of postural body space” (e.g. Paillard, 1991a). This type of processing of spatial information would be related to the “sensorimotor mode” according to Paillard’s terminology and to the “direct mapping hypothesis” (e.g. Baud-Bovy & Viviani, 1998). In contrast, an extraction of extrinsic target coordinates (see “target position hypothesis”, Baud-Bovy & Viviani, 1998) would rather reflect “an internal representation of environmental

space" (e.g. Paillard, 1987) and thus, the "representational mode" of processing (see 1.1 for the according link). As suggested by Rossetti and Pisella (2002) and confirmed by our data, both response modes can be considered as complementary and may differ in their temporal dynamic.

However, all the results cannot be explained with only two different types of processes, whatever their exact nature may be. Especially since the EEG data strongly suggest at least three different mechanisms of information retention and / or motor planning. This fact cannot be explicitly predicted neither by the dual-mode approaches nor by the conceptual planning schemes mentioned previously.

1.3 Subsumption of results within a general framework of memory research

The idea that processing may change dependent on time between stimulus and response is far from new. Within the psychological memory research, the dissociation between an early sensory and a short-term memory (STM) has a long tradition (e.g. Pashler & Carrier, 1996). The sensory store is assumed to be associated with an initial maintenance of a stimulus event for immediate processing (e.g. Massaro & Loftus, 1996). It is characterized by a parallel analysis of a large capacity operating on the level of physical stimulus attributes within a time range of a few hundreds milliseconds. These features are traditionally considered to be in contrast with more durable retention mechanisms, like STM associated with attention, capacity limitations, a more abstract processing, etc. More recently, several findings indicated a further "intermediate" perceptual storage within the visual modality, which takes place between the early sensory and the classical STM (Magnussen, Idas, & Myhre, 1998, Magnussen & Greenlee, 1999, Magnussen, 2000, Pasternak & Greenlee, 2005). These "perceptual online representations" were attributed to a set of parallel, feature-selective mechanisms, which has limited capacity and codes basic dimensions of the visual stimulus. Within this research field, it was repeatedly shown that a few seconds and/or a few hundred milliseconds intervals may be critical for consolidation and integration processes (e.g. Brockmole, Wang, & Irwin, 2002, Jiang, 2004, Jolicoeur & Dell'Acqua, 1998, Chun & Potter, 1995), the dissociation between perception and short-term memory (e.g. Magnussen, et al., 1998), the dissociation between the early sensory mechanisms and a more "durable storage" (e.g. Phillips, 1974, Pashler & Carrier, 1996).

On the other hand, similar time ranges were associated with changes in sensorimotor processes within the “motor” research domain relating to visuomotor performance (e.g. Goodale, Jakobson, & Keillor, 1994, Vaillancourt & Russell, 2002, Bradshow & Watt, 2002, Elliott & Madalena, 1987, Westwood, Heath, & Roy, 2001, Rossetti & Pisella, 2002), the retention of efferent information (Ito, 1991), kinesthetic pointing (e.g. Rossetti, 1998) and effects of visual illusions on motor responses (e.g. Bridgeman, Gemmer, Forsman, & Huemer, 2000, Glover, 2004) among others.

Having possible caveats relating to overgeneralization in mind, one may assume that the results obtained in the two research areas may describe similar phenomena. In fact, a transfer of the memory-structure assumptions to the results and conclusions derived from the analyses of motor activity may explain the most of our as well as resolve some discrepant results reported previously. Figure 1-1 shows a possible relation between proposed representation systems and motor planning processes. According to this, information passes at least three different processing stages with distinct characteristics in the range of seconds (e.g. sensory memory, perceptual online representations and short-term memory). The main idea relating to motor planning processes is that the motor system can use information from all of these hierarchical levels. If response is required immediately, a type of “low-level” planning occurs, which selects relevant information from the initial short-lived and “fading image” of an event (i.e. from the sensory memory representation). In case of kinesthetic matching tasks, this representation probably contains the whole dynamic of an “encoding” movement. Thus, the planning would imply an access to such dynamic representation and may consequently be expressed in the reproduction of the first movement rather than in extraction of spatial target coordinates and reprogramming of movement parameters. In contrast, if the response is delayed by several seconds, one may assume that this initial source of information is not more sufficient to provide adequate parameters of a stimulus location due to the fragility of dynamic information and capacity limitations of the system. Consequently, the planning should rather rely on static sources, like on spatial target representation, whose retention may depend on attention, categorization and other “higher level” processes. A characteristic functional feature of the “perceptual” level seems to be less obvious. However, the EEG data strongly suggested that neuronal mechanisms involved in retention of information in the time scale of about one second are distinct from those obtained during shorter and longer delay conditions. According to Rosenbaum et al. (1999), one may speculate that the reproduction of final postures may play an important role here.

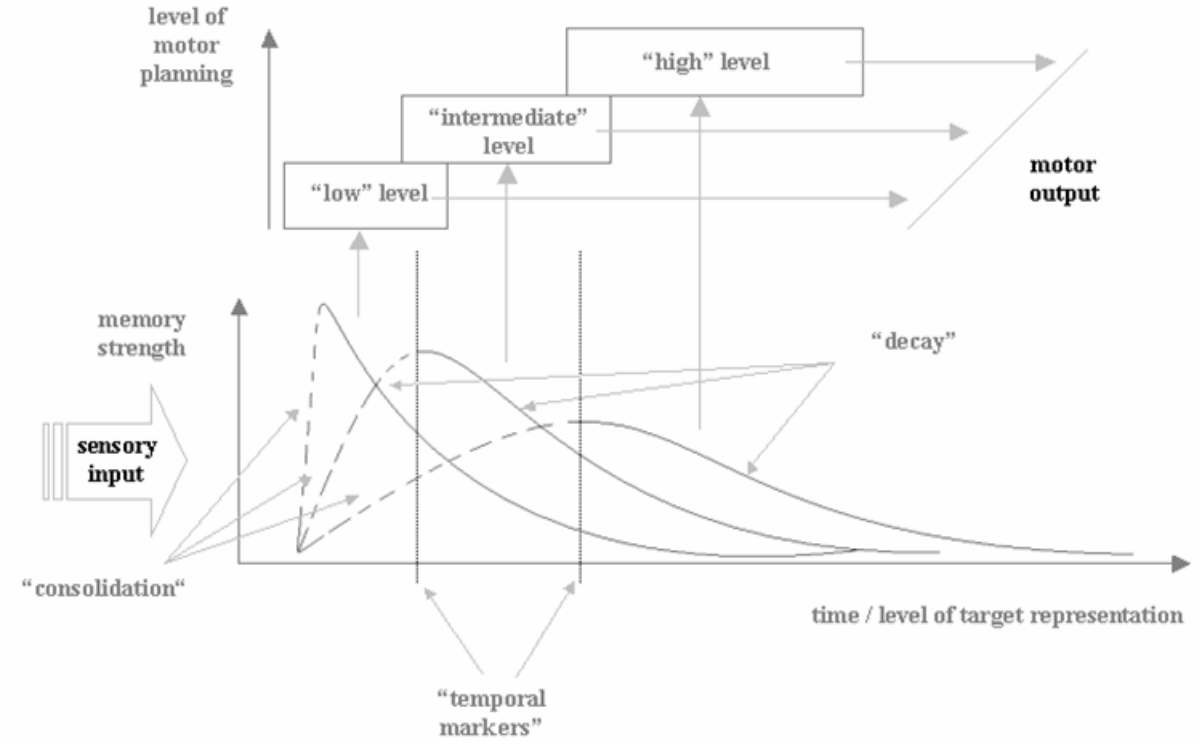

Figure 1-1. A crude course of information flow between an external stimulus and the according response. Three distinct sensorimotor loops are assumed to be potentially involved in the range of seconds. If response is required "immediately" after a stimulus (i.e. within a few hundreds milliseconds), motor planning processes select relevant information from an early sensory representation (i.e. from "sensory memory"), which maintains basic physical attributes. Thus, planning is associated with a type of "how to get there" (e.g. Paillard, 1991b) processes, rather than with "what" or "where" representations. Accordingly, such a sensorimotor loop may reflect a "direct" sensorimotor system (e.g. "vision-for-action"), in which sensoritopic stimulus and effector information is coupled directly (e.g. on the level of eye coordinates, see e.g. Buneo et al., 2002; or on the level of "body schema", see e.g. Paillard, 2005). If response is delayed by several seconds, stimulus information is assumed to be on a more abstract level, including the contribution of categorization, memory and other "higher" cognitive processes. Consequently, motor planning may occur on a higher level, like in a "configural mental space" (e.g. movement planning to a kinesthetically defined spatial location would rely on a representation of a target in an extracorporal space, see "target position hypothesis", Baud-Bovy & Viviani, 1998). The existence of an intermediate representational system (e.g. "perceptual") operating between approximately 500 and 2000 ms is mainly supported by the two EEG-studies. Although, the functional characteristics of according stimulus representations and motor planning processes are not clear, and may share similarities with the others, the detected electrophysiological markers of retention and / or planning differed strongly from those obtained in shorter and longer delay conditions.
The initial target information is assumed to decay exponentially. However, this decline occurs within three different functional systems (e.g. sensory, perceptual and short-term memory). Thus, a complete account of information retention in the time range of seconds would imply at least three different functions (e.g. with different slops). Some indices for these processes were detected by the behavioral experiments (see the first manuscript). The term "consolidation" is used for progressive stabilization of a memory trace (e.g. buildup of a uniform percept from basic physical features). The "temporal markers" indicate assumed latencies of changes in processing and /or representational characteristics. They may reflect an "abrupt" switch from one mode to another or a rather continuous shift of relative dominance of certain information sources within the given memory trace (e.g. from *dynamic* to *static* processing).

Although the visuomotor processes were investigated to a less extent within the current dissertation, the performed EEG study again seems to argue for rather three functionally distinct mechanisms operating within the first seconds after stimulus presentation. Moreover,

they appear to fit well into the proposed linking between memory and motor planning. When a response was required 200 ms after stimulus offset, the motor planning phase was characterized by “evoked alpha activity” over early visual areas, which seems to be closely related to the iconic mechanisms. The analyses of the middle delay condition (1 sec) appeared to suggest that posterior regions are deactivated in a distance specific manner during the retention interval. According to the literature, we concluded that such a process may be associated with the retention of information on a mnemonic (i.e. perceptual) level. When hand movements were initiated 5 seconds after stimulus presentation, a stronger involvement of lateral frontal regions during the retention period and an additional positive component during the motor planning phase over posterior areas was obtained, which seemed to reflect retention and recall processes within the classical STM.

Since no directly comparable studies were identified and some proposed relations are rather abstract and may not be compelling, all results and driven conclusions should be considered with caution. Consequently, the course of processes illustrated in Figure 1-1 is an attempt to integrate our and other relating results from different research domains rather then an explicit model. I assume that several previous findings as well as recent concepts relating to the general nature of perception-action integration (e.g. Fuster, 2004) are compatible with the given schema. However, given the complexity and plurality of sensorimotor architecture and functionality, the present experiments hardly indicate an aspired solution for all the questions, but rather only a basis on which one may begin.

2 Behavioral Experiments: “Delay dependent changes of sensorimotor processes in a motor memory task”

2.1 Introduction

The peripheral receptors within muscles, tendons, joints and skin measure several parameters, like position, direction and velocity and thus, provide us with a rich source of information about the position and the motion of a limb. Moreover, this initial kinesthetic information may be transformed into an extrinsic representation and may also inform us about locations of objects and / or our body parts in external space (e.g. Klatzky & Lederman, 2003). Imagine a situation, where we drink a cup of coffee while reading a newspaper and put the cup on a desktop without seeing it. One may assume that the final position of the cup is encoded in respect to an external point (e.g. fixed on body midline, shoulder or another external cue). However, if the body position remains unchanged, we should also be able to reach the cup correctly by performing the previous movement again (i.e. by using the whole dynamic information provided by the first movement). Moreover, we may also produce quite different movements, which aim at the same final angular configuration of joints and can reach the cup. What kind of representation does the brain maintain and use for the planning of a motor act in similar situations?

A line of research, dealing with these kind of questions, emerged in the late 60s (e.g. Laabs & Simmons, 1981). In a typical task, known as linear positioning, the subjects moved their arm in a straight line or curve until a stop (or it was moved by the experimenter) and tried to reproduce the final location or the moved distance from a new starting position after a delay. The subjects were usually prevented from seeing their hand and targets during the experiments. Several early studies indicated that final position reproduction is better than distance reproduction, suggesting that static limb and / or target position cues are superior to dynamic kinesthetic information. According to one view, the advantage of location reproduction over extent reproduction may reflect a more abstract encoding within a spatial coordinate system (e.g. Smyth, 1984, Millar,1994). However, due to several methodical problems these early findings did not reveal a consistent picture (e.g. Laszlo, 1992). Rosenbaum et al. (1999) favored for instance a body state hypothesis, suggesting the reproduction of final posture as central in position matching tasks. According to this, the new starting position during the test phase in early studies led to a decrease in performance in the distance conditions since the final posture could not be adequately adopted.

The question of the nature of information used for motor planning in visuomotor as well as in kinesthetic research domain is still ongoing and has recently been discussed in the framework of “frames of reference” (e.g. Soechting & Flanders, 1992).

Tillery, Flanders, & Soechting (1991) analyzed the error patterns in experimental conditions, where subjects were asked to reproduce a target location, previously defined by the passive displacement of a hand, either by an active hand movement (in the dark) or by using a pointer (under dark and light conditions). Additionally, in a control condition, the subjects had to indicate the location of a briefly presented visual target. The results from these experiments led the authors to believe that kinesthetic information is rather used, when it is represented in arm orientation parameters, than when it is transformed in a spatial representation of the hand’s location. Similar conclusions were drawn from experiments of the same research group (Tillery, Flanders, & Soechting, 1994), in which spatial position of the passively displaced right hand was reproduced by the left hand. The authors distinguished the sensorimotor transformations in kinesthetically guided tasks, which are assumed to occur within the “intrapersonal” space, from those underlying visuomotor performance, which require “extrapersonal” coordinates.

In contrast, Baud-Bovy and Viviani (1998) argued for a “target position hypothesis”, whereby the initially kinesthetically defined target location is translated into an extrinsic coordinate system, in which planning processes take place. The task was to reproduce a target position that was previously defined by guiding a subject’s left or right index fingers with a robot. The reproduction movements were performed with the right hand. The authors obtained a strong similarity of postures, constant and variable error patterns, irrespective of whether the right or left hand was used in the locating phase. These observations were interpreted in terms of the hypothesis mentioned above. However, postural variability in the locating phase explained the corresponding variability of the pointing phase to some extent, indicating that postural memory trace was still available during reproduction.

Based on results from similar experiments in another study, the authors (Baud-Bovy & Viviani, 2004) suggested a model according to which several representation formats exist: a sensorimotor (dynamic representations including kinesthetic input and efferent commands), a perceptual (abstract representations including a class of dynamic representations) and a motor (groups of potential movements to a given endpoint). Nevertheless, the movement planning to a kinesthetically defined target position was assumed to occur on the representational (i.e. perceptual) level.

By using “active” and “passive” presentation of the target in a kinesthetic matching task, Adamovich, Berkinblit, Fookson, and Poizner (1998) reported evidence for a “mixed” control strategy, which was associated with using all available information including intrinsic and extrinsic sources.

As shown, these more recent findings are also not unambiguous and partly indicate quite different scenarios for similar experimental situations. Following the results from the visuomotor domain (see e.g. Battaglia-Mayer et al., 2003 for a review), which suggest that the use of a specific mechanism (e.g. a specific frame of reference) is task and context dependent, one may expect a similar pattern of results also in the kinesthetic modality. If so, are there certain task situations which benefit one specific process over others? Some indices for such a general characteristic are reported from another line of research.

Paillard et al. (1983) described a patient, who was able to correctly locate tactile stimuli with the left arm, which were applied to the deafferented right arm and, consequently, could not be perceived. Similar results were obtained by Rossetti and colleagues (see Rossetti, 1998 and Rossetti & Pisella, 2002, for reviews) in another patient with tactile and proprioceptive deficits on the right side of body. Despite the disability to perceive stimulation as indicated by verbal reports, the patient showed a residual ability to perform movements with the left hand to tactually and proprioceptivelly defined targets presented to the deafferented body side. This phenomenon labeled as “numbsense” is considered as analog to “blind sight” obtained in the visual modality and is often cited among a considerable body of other findings as evidence for the functional and / or neuronal dissociation of two modes of sensorimotor processes (for review see e.g. Goodale et al., 2004, Jeannerod et al., 1995, Norman, 2002, Paillard, 1991a, 1991b, Rossetti & Pisella, 2002, Rossetti, 1998).

The processing of absolute metrics of an object, which are primarily relevant for a motor response, is ascribed to a direct mode, labeled as “sensorimotor”, “pragmatic” or “vision for action / how”. The “cognitive” mode (also labeled as “semantic”, “representational”, “vision for perception”) is assumed to create an internal representation by binding of stimulus attributes, allowing the maintenance of information over a longer time scale. Among several dichotomies, which are used for the dissociation of the mentioned mechanisms (see e.g. Norman 2002), time aspect seems to play an essential role (Rossetti & Pisella, 2002). The authors reported a series of pointing experiments, in which the delay between a passive displacement of the hand and the reproduction movement was varied. Delay dependent changes of errors were obtained. Variability ellipses were oriented in the direction of the pointing movements, when immediate reproduction was required. In contrast, delayed

movements (initiated after 8 seconds) were associated with ellipses oriented towards other targets (orthogonal to movement direction).

Moreover, the patient mentioned previously lost the ability to guide a movement on the basis of unaware information, when the stimulus response delay extended 2 seconds. Similar results in the visual modality are reported by Goodale et al. (1994). The authors obtained that the obvious ability of an agnostic patient, whose perceptual discrimination performance was dramatically impaired, to correctly scale his grasp, disappeared after a delay interval of 2 seconds. On the contrary, an ataxic patient showed a “paradoxical” increase of pointing accuracy when a delay of 5 seconds was introduced, as compared with immediate performance (Milner et al., 1999).

Thus, independent from the suggested interpretations, these results seem to indicate that motor control mechanisms and / or sensorimotor processes can change dependent on an interval between a stimulus and a corresponding response.

Starting with these findings we conducted a series of experiments, in which we investigated the influence of varying delay duration on memory of kinesthetically defined spatial locations. We used an apparatus allowing one-dimensional hand movements on the horizontal plane along the mid-saggital axis of the trunk. The general task comprised an “encoding phase”, during which the blindfolded subjects moved a handle until a stop and then back, and a “reproduction phase”, in which the stop position (or movement distance in Experiment 3) had to be reproduced by another hand movement.

In the first two experiments we investigated the influence of mental and motor interfering activity performed during the interval between the “encoding” and the “reproduction” phases. The delay was adjusted to approximately “0” (immediate reproduction) and “8” (delayed reproduction) seconds in both experiments. The subjects were asked to judge the distance from the staring position to a stop position verbally in the first experiment. In the control conditions no verbal reports were required. In the second experiment we contrasted conditions, in which after the “encoding” movement an interpolated movement with the same hand (right) was performed, with other conditions, in which the opposite hand was used for the interpolation task.

There are some indices from early studies that certain aspects of encoding / maintenance are differently affected by mental and motor distractors. Dynamic kinesthetic cues (i.e. distance reproduction) seem to depend on central attentional capacity demanding by interpolated mental activity to a lesser extent, as location reproduction (e.g. Laabs, 1973).

Studies, comparing the performance of location and distance reproduction dependent on interpolated kinesthetic activity, on the other hand, revealed that both reproduction modes can be selectively affected by a motor distractor (Laabs, 1974, Haagman, 1978). The distance of the interpolated activity proved to be critical for distance reproduction, while the end locations of distractor movements seemed to primarily affect location reproduction (see also Smyth,1984, Laabs & Simmons, 1981 for reviews).

Although there are some other divergent findings related to this topic (e.g. Laszlo, 1992), we used these results as a starting point and proposed that if immediate and delayed responses rely on “qualitatively” different mechanisms, then the effect of interpolated activity should depend on delay duration.

Moreover, initial kinesthetic information is assumed to be effector specific (or to be fixed on limb segments, see e.g. Soechting & Flanders, 1992). It was also reported that the retention of relevant information in the somatosensory modality may involve different neuronal substrates dependent on the duration of retention interval. Harris, Harris, and Diamond (2001) reported a series of experiments, in which vibration stimuli to different fingertips, on the same or on the other hand, were applied and frequency comparisons were required. The authors obtained that under short retention intervals (< 1sec) the judgments were most precise, when the same finger was stimulated. During longer delay intervals the subjects showed comparable performance independent from whether the same finger or corresponding fingers of different hands were stimulated. Additionally, when retention interval was 1 second, accuracy decreased with an increase in the distance between the vibration sites (i.e. distance between the first stimulated finger and a neighboring finger stimulated after a delay). This relation was no longer present when the delay interval was 2 seconds. Based on these results the authors suggested that, dependent on delay duration, different regions of somatosensory cortex may be involved in tactile short-term memory. According to the authors, the retention of relevant representation under short delay conditions (<1sec) appeared to be independent from the involvement of the opposite hemisphere (the authors emphasize the role of S1 in such mechanisms). In contrast, a longer retention of tactile information seems to be associated with mechanisms relying on interhemispheric connections.

Following these findings, we assumed that during the short delay condition interpolated movements performed with the same hand (right) would interfere stronger with initial kinesthetic representation as interpolated movements with the opposite hand (left). On the contrary, during the longer delay condition we did not expect any differences.

In a third experiment, we varied the delay duration again (“0” vs. “8” sec) and asked to reproduce the position of the stop or the covered distance from a new starting position. As already mentioned, the majority of studies supported the view that static position cues are superior to dynamic kinesthetic information. However, when immediate reproduction was required, the performances in both task situations appeared to be comparable (Hagman, 1978, Hagman & Francis, 1975). We aimed to replicate these findings and according to them we expected similar results for both reproduction conditions, when delay was short and a stronger decrease in performance in the distance reproduction condition, when the long delay was used.

In the last two experiments we asked the subjects to reproduce the position of the stop and adjusted the delay interval to approximately “0”, “200”, “400”, “600” and “800” ms in Experiment 4 and to “0”, “1”,”2”, “4”, “6” and “8” seconds in Experiment 5. We aimed to pursue the performance without any additional constrains. The main question of interest was whether indices for time dependent changes of processing characteristics in a given task are detectible. We did not find comparable studies using kinesthetic stimulation. Consequently, the approach was primarily exploratory.

In all experiments we used constant and variable error measures as dependent variables. Additionally, correlation analyzes and analyzes of some kinematic parameters were performed, if it appeared to be appropriate. In order to prevent practice effects, each experiment was performed on a different sample of subjects, who were prevented from seeing the used apparatus before as well as during the experiments.

2.2 Experiment 1: “Mental distraction”

2.2.1 Methods

Subjects

Twenty-two right handed subjects participated in the present study. They received course credit at the end of the experimental session. Two subjects were excluded from the analyses due to a large number of movement artifacts resulting from difficulties in the handling of experimental apparatuses. The final sample comprised 4 males and 16 females, with ages ranging from 19 to 25 years (mean age 21).

Paradigm and task

The subjects were blindfolded and set in front of a linear track device, allowing one-dimensional movements of a pen-like, lightly moveable handle on a horizontal plane. Eight lift-magnets were mounted in the device in distances between 14 and 35 cm in front of the starting position (3cm between successive magnets) and were used to stop movements at a certain location. The starting position was defined as the nearest possible handle location in respect to the body (approximately 10 cm). Earphones were used to transmit acoustic signals. Before and during the experiment, the subjects were prevented from seeing the apparatuses. A trial started with an auditory warning stimulus, followed after a fixed interval of three seconds by a first imperative GO-signal (250Hz). The subjects were asked to move the handle rapidly until the stop and then immediately backward. After the second GO-signal (250Hz) participants had to reproduce the stop position as accurately and rapidly as possible with another hand movement. Two delay intervals were used. In a pilot experiment we measured the response times of the first movement (including reaction times and movement durations of forward and backward movement) in the range between 1.2 and 1.5 seconds in a similar experimental situation. In the present study we intended to compare immediate reproduction with a delayed one, and thus we presented the second imperative signal either 1.5 seconds after the first in one condition (labeled as “0”) or after 9.5 seconds in another one (labeled as “8”).

The subjects were additionally asked to estimate the movement distance until the stop verbally during the delay interval under two further conditions, in which this delay manipulation was also implemented. In the longer delay condition, an additional auditory

signal (1000Hz) occurred 4.75 seconds after the first imperative GO-signal. During the short delay condition, judgments were required immediately after the first backward movement. We used an 8 target locations (stop positions) x 2 delays (“0” and “8”) x 2 distractor (“unfilled” and “judgment”) within participants block design. The experiment was divided into four blocks, each of them consisting of 24 trials (8 locations x 3 repetitions). The delay interval and the type of distractor were held constant within each block ((A) delay “0” & “no verbal judgment”, (B) delay “8” & “no verbal judgment”, (C) delay “0” & “verbal judgment”, (D) delay “8” & “verbal judgment”). Eight targets were presented randomly with the constraint that the whole sequence of positions should be completed before another repetition. The order of blocks was randomized for all participants. Each subject performed four practice blocks, including all conditions.

Data analysis

Movement trajectories of the manipulandum were recorded with an ultrasound motion device (ZEBRIS, CMS 20). The data were sampled at 100Hz initially and analyzed with software using Lab View codes (National Instruments, Graphical Programming for Instrumentation). Constant and variable error measures were defined as dependent variables and analyzed statistically by using repeated measures analyzes of variance (ANOVAs) with “target distance”, “delay” and “distractor” as factors.

Constant error score reflects the mean deviation of the moved distance from the target distance and was computed by averaging response errors, whereas the sign of each error was retained. In order to measure the response consistency, we calculated a coefficient of variability according to: $V = (SD / M) * 100$, where SD is the standard deviation about the mean movement endpoint (M). Due to a small number of repetitions, we treated two neighboring target positions as one and defined a reduced (halved) number of levels for factor “distance” in the ANOVAs.

Moreover, to compare the systematic verbal errors (computed analog to constant motor errors) with constant motor errors, we performed an ANOVA with “delay” (“0” and “8”), “distance” (8 target locations) and “response mode” (“verbal” and “motor”) as within subjects factors. The same analysis was also run with standardized (z-transformed) values in order to counteract the possible violations of ANOVA requirements.

For all analyzes, significance was tested on an alpha level of 0.05 and degrees of freedom were adjusted according to Geisser and Greenhouse (1958) when violations of the assumption of sphericity were obtained[1].

Additionally, we investigated the relation between verbal reports and motor responses by computing Pearsons' correlation coefficients between the amplitudes of the "encoding" movement and the verbally reported distances. Similarly, systematic judgment errors were correlated with corresponding constant error values of the reproduction movement. Furthermore, partial correlation coefficients were used to compare the effect of judgments on motor reproduction, where distance of the first movement served as the control variable. All correlation coefficients were computed on the single trial basis.

2.2.2 Results

Table 2-1 illustrates the results derived from the ANOVAs performed on constant and variable error measures.

Table 2-1. Main effects and interactions of performed ANOVAs, *p<.05, **p<.01.

	Constant error			Variable error		
Effect	df	F	P	df	F	P
"delay"	1,19	**17.45****	**.001**	1,19	**41.95****	**<.001**
"distractor"	1,19	.00	.989	1,19	.11	.747
"distance"	7,133	**22.62****	**<.001**	3,57	**59.13****	**<.001**
"delay x distractor"	1,19	.91	.353	1,19	**5.50***	**.030**
"delay x distance"	7,133	**4.90****	**.001**	3,57	1.80	.157
"distractor x distance"	7,133	1.34	.263	3,57	.94	.429
"delay x distance x distractor"	7,133	1.17	.322	3,57	1.03	.384

Both error types were affected by the delay manipulation, as indicated by the significant main effects of the factor "delay". The longer delay conditions were associated with an increase in response variability and a reduced degree of overshooting on average, compared with the immediate reproduction (see Figure 2-1). However, these differences were dependent on distance or distractor manipulation.

The significant "delay x distractor" interaction of the variability analysis showed that the response consistency was differently affected by the verbal reports dependent on the delay condition. When the delay interval was long, verbal judgments caused a higher response

[1] We report uncorrected degrees of freedom and corrected P values in the result section.

variability compared with the unfilled condition. In contrast, when the delay was short, an opposite trend was observable (see Figure 2-1 (A) for means).

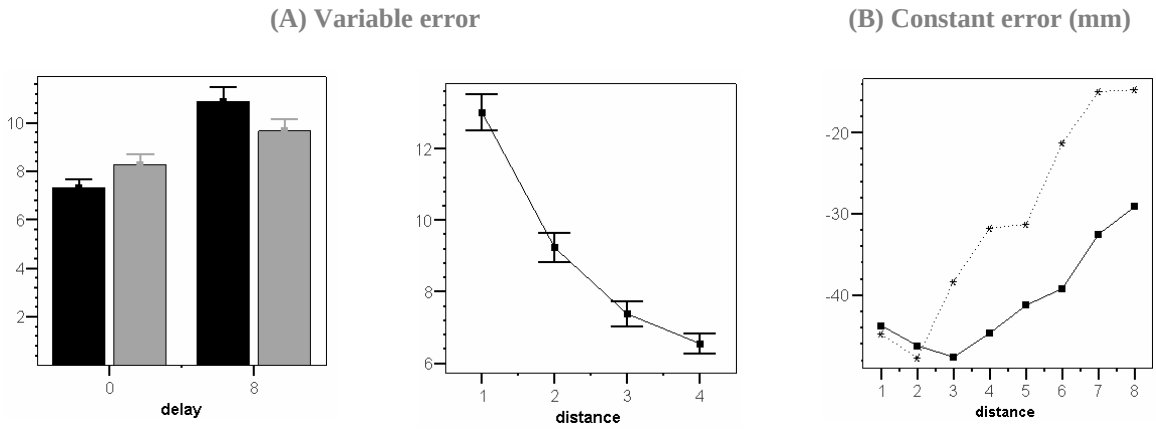

Figure 2-1. (A) Variable error. *Left*: Mean values of variability coefficients with corresponding standard error scores (■ - judgment conditions, □ - unfilled conditions). *Right*: mean values averaged according to four target distances (see methods). (B) Mean constant error values (—■— short delay, ···✳··· long delay). Negative values represent the magnitude of overestimation.

Moreover, an increase in distance was associated with a significant decrease in response variability (Figure 2-1 (A)).

In all conditions, the mean amplitude of the reproduction movement was higher than the real amplitude of the target distance (i.e. the subjects overestimated the target distance on average). There was a tendency towards higher overshooting with a decrease in distance (see Figure 2-1 (B)). In the longer delay conditions, the subjects missed the targets to a lesser extent on average. However, the first two target distances were not affected by the delay manipulation, while with a further increase in target distance a trend towards a decrease in overshooting with an increase in delay duration was obtained.

The reported distance estimations were closely related to the extent of the first movement on average (see Figure 2-2 (A)), indicating that subjects were able to discriminate between eight target positions. While the subjective judgments correlated strongly with the distance of the first movement (r = .74 ("delay 0"), r = .75(delay 8"), Ps < .001), the distance of the reproduction movement was unaffected by the reported values (partial correlation coefficients[2]: r = .05, P = 0.281 ("delay 0"); r = .03, P = .511 ("delay 8"). Moreover, systematic deviations from exact reproduction in both response modes were independent of each other ($r_{(total)}$ = -.006, P = .866; $r_{(\text{"delay 0"})}$ = .034, P = .464; $r_{(\text{"delay 8"})}$ = -.010, P = .835).

[2] Note: distance of the encoding movement was held constant in this analysis.

Furthermore, we compared motor and subjective errors by using an ANOVA with “delay” (2 levels), “distance” (8 levels) and “response mode” (2 levels: verbal and motor) as factors. The corresponding results are depicted in Table 2-2 (A).

The main factor “response mode”, a “response mode x delay” and a “response mode x distance” interactions became significant, indicating differences between both error types which were dependent on delay and distance manipulation. As previously mentioned, motor responses were associated with an overestimation of target distance. In contrast, the subjects underestimated the target position by verbal reports. Moreover, when the delay interval was prolonged, a decrease in underestimation of judgments and a decrease in overestimation of motor biases was obtained (see Figure 2-2 (B) for mean values). In addition, while an increase in distance was rather expressed in a tendency to less overestimation, when motor response was required, verbal judgments showed rather a decrease in underestimation with an increase in target distance (see Figure 2-2 (C)).

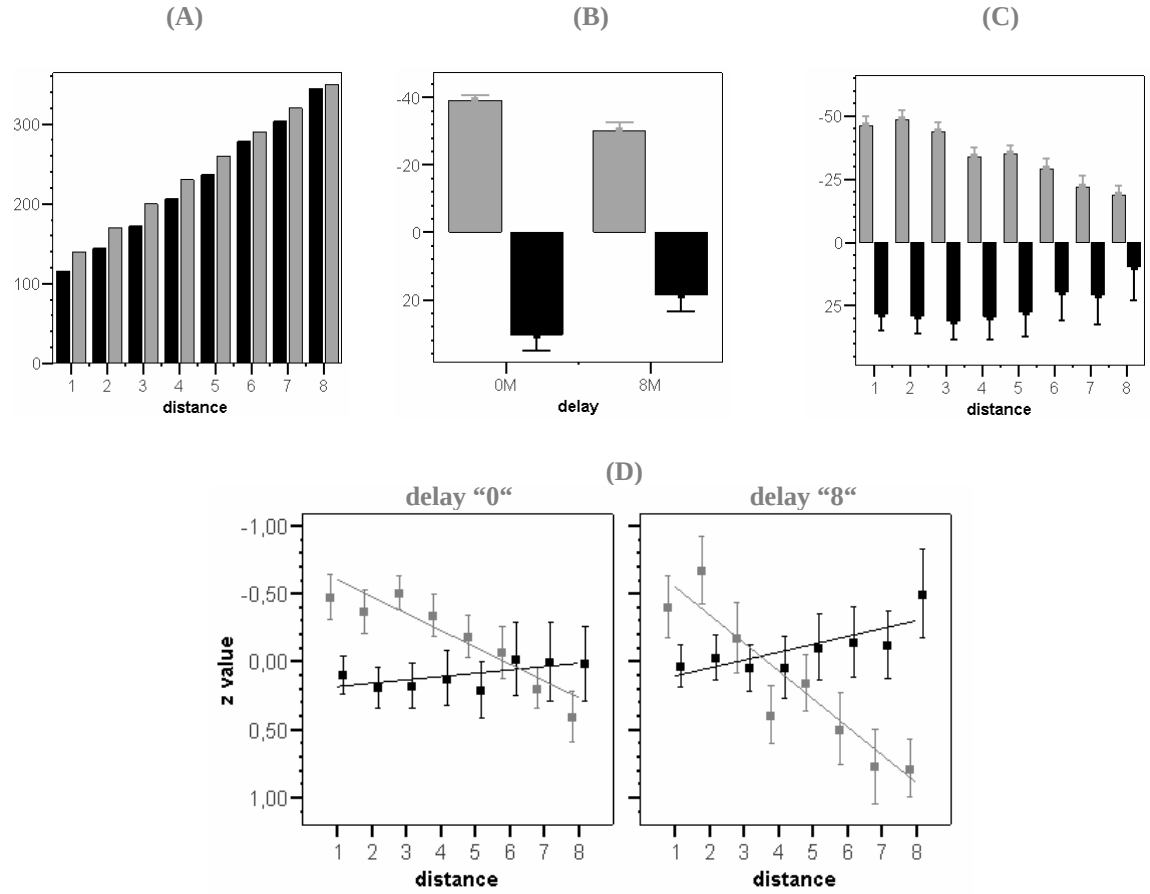

Figure 2-2 . (A) Mean distance judgments (■) and real movement extent of the first movement (□) as function of eight target positions. (B) and (C) Mean systematic deviations of verbal reports (■) and motor responses (□) from exact reproduction (“0”). (D) Mean Z scores of verbal (■) and motor errors (□) according to the distance and delay manipulations. Note: all values are computed based on data from conditions, in which verbal distance estimations were required; all values on the Y axis in (A), (B), and (C) are in mm; error bars reflect standard error.

A similar analysis performed with standardized values (z scores) suggested further that in addition to the response mode specific delay and distance effects (see also above), delay dependent changes of bias according to the eight target conditions were also dependent on the type of reproduction (due to a significant "response mode x delay x distance" interaction, see Table 2-2 (B) for statistical results and Figure 2-2 (D) for means).

Table 2-2. Statistical results of two ANOVAs applied to the raw (A) and standardized (B) values of verbal and motor systematic errors.

		(A)		(B)	
Effect	df	F	P	F	P
"response mode"	1,19	**21.39****	**<.001**	0.00	1.00
"delay"	1,19	.36	.556	1.73	.204
"distance"	7,133	.90	.421	**5.45****	**.003**
"response mode x delay"	1,19	**8.50****	**.009**	**9.67****	**.006**
"response mode x distance"	7,133	**7.53****	**.002**	**15.40****	**<.001**
"delay x distance"	7,133	1.91	.072	**2.53***	**.018**
"response mode x delay x distance"	7,133	1.95	.117	**2.77***	**.010**

2.2.3 Discussion

By analyzing the response variability in the present experiment we obtained that verbal estimations of the target distance caused a decrease in response consistency, compared with the "unfilled" condition, when the delay interval was long. When the delay was short, an opposite trend was detectible. Since variable error indicates an "index of forgetting" (Laabs & Simmons, 1981) or "strength of the memory for movement" (Smyth, 1984), this result may suggest that the interpolated mental activity shared similar cognitive resources with maintenance processes of the acquired information, but only from a certain level of processing and / or from a certain point of time. The tendency towards more response consistency under the short delay condition seems to be less plausible and may indicate an increase in a general arousal level, when a verbal judgment is required.

At first view, these results seem to confirm the dual-system models described in the introduction ("sensorimotor" vs. "cognitive"). One may assume that the lack of interference under the short delay condition may result from the independence of "direct" sensorimotor processing from attentional capacity.

However, within this research it was also suggested that the "action" system may be inhibited by a cognitive representation of the action goal (see Rossetti & Pisella, 2002 for a review). The motor ability of "numbsense" and "blindsight" patients, mentioned in the introduction, was lost if they were asked to produce a verbal report simultaneously to the action (Rossetti,

1998, Rossetti, Rode, & Boisson, 1995). Immediate pointing performances of normal subjects towards proprioceptive targets were not more different from the delayed responses, when a verbal report of the target number was additionally required (Rossetti & Regnier, 1995, see also introduction). Unlike the target number reports, a simple downward counting did not show a similar effect. Similar results are reported by Bridgeman, Peery, and Anand (1997, see also Bridgeman, 2002). A visual illusion ("induced Roelofs effect"[3]) affected the immediate pointing responses if the subjects were asked to judge the perceived target location in the same trial. Without cognitive judgments, half of the subjects were unaffected by the illusion, when response was required immediately.

Although our experiment seems to be comparable with the last mentioned, we did not find evidence for such interaction in the present study. The verbal reports did not affect the amplitude of the reproduction movements neither under short nor under long delay conditions. This result, together with the variability measures, seems to suggest that both response modes may possibly demand similar resources (i.e. general attentional capacity), but use different "codes" under given task conditions (e.g. converting kinesthetic information into an allocentric visuo-spatial representation for verbal judgments vs. the using of kinesthetic and / or extrinsic egocentric representation for movement planning). This hypothesis seems also to be supported by the delay and distance specific differences of systematic errors in both response mode conditions.

Moreover, by following the results from early motor memory studies indicating a preference of location cues over dynamic distance information in longer delay conditions, as well as some findings, where interpolated mental activity rather affected the position reproduction (e.g. Laabs & Simmons, 1981), our results would support the view that under a long delay condition, the motor planning would rather be based on static information sources. Additionally, it is traditionally assumed that kinesthetic cues can not be rehearsed (Posner, 1967) and that the advantage of position reproduction over distance reproduction derives from a possibility for a more abstract coding within a spatial frame of reference, as compared with purely kinesthetic coding of distance (e.g. Smyth, 1984, Millar, 1994, but see Rosenbaum et al., 1999 for an alternative interpretation). If so, then the static information interfering with verbal judgments in the long delay condition of the present experiment would be extrinsic.

The analysis of the constant error measures revealed a quite unusual picture. We obtained that subjects showed a tendency to overestimate the target distance and these biases increased with a decrease in target distance. Although overshooting in kinesthetic tasks is reported (e.g.

[3] When a small visual target is surrounded by a large frame positioned so that the frame's center is offset from the observer's midline, the perceived location of the target is shifted in the direction opposite the frame's offset.

Tillery et al. 1994, Wolpert, Ghahramani, & Jordan, 1995), the mentioned distance specific characteristic of errors is rather unexpected. We assume that this pattern may be a result of the used test arrangement. The subjects were blindfolded and were asked to perform rapid uncorrected hand movements until a stop during the “encoding phase”. The stop position was unpredictable presumably leading to the selection of amplitude as default. During practice blocks the subjects became familiar with the range of targets and, thus, they should initially aim for a rather far position in order to reach all targets. The results of Experiment 3 seem to confirm this hypothesis (see below).

It was suggested that initial hand position estimation after a movement is based on an integration of motor command information and sensory feedback signals (Wolpert et al. 1995, van Beers, Baraduc, & Wolpert, 2002). If the encoding movement is really planned according to a far position, one would expect that efference copy information is successively less deviated from proprioceptive feedback. Consequently, the proposed updating process would be biased in the direction of a movement of higher amplitude, possibly leading to substantial overshooting in short distance conditions. This distortion should decrease with an increase in target distance, since the magnitude of the conflict between efferent and afferent information sources would be reduced. In addition, the obtained decrease in variability with target distance may indicate changes of encoding efficiency associated with different amounts of this conflict. As a result, one would expect an increasing stability of the memory trace with the target distance.

Moreover, the Kalman filter model mentioned above (Wolpert et al. 1995) predicts a decrease in overshooting with an increase in dominance of sensory feedback. According to this view, one may assume that the initial phase of encoding movement is mainly controlled by efferent signals and a successive later braking of movement would be associated with an increasing dominance of sensory feedback in the initial estimation of hand position. Thus, our result may simply reflect a time dependent shift of initial coding in the direction of a decreased influence in efferent and an increased influence in afferent signals on the estimation of hand / target position. Both alternatives do not contradict and would explain our results.

We also obtained an effect of delay on the constant error that was expressed in a reduced overestimation when the retention interval was long (this was true for six of eight target positions). This result is in line with several finding from motor memory research indicating a shift of constant error in the direction of “undershooting” over an empty interval, which was associated with changes of perceptual processing (e.g. Laabs & Simmons, 1981).

2.3 Experiment 2: “Motor distraction”

2.3.1 Methods

Subjects

The subjects were twenty-two right handed students of the University of Marburg, who received course credit for their participation. Due to an insufficient quality of data, one subject was excluded from the analyses. The remaining participants were 16 females and 5 males between 18 and 35 years of age (mean age 22).

Paradigm and task

The experiment was performed with the same apparatus that was described in the previous section. Paradigm and task were also highly comparable with those of the first experiment. The essential difference to the previous study referred to the distractor manipulation. Instead of verbal judgments (and “unfilled” conditions), the subjects were asked to perform a short interpolated movement of approximately 10 cm with their left vs. right hand.
The experiment was divided into four blocks again: 1) delay “0” & “right hand”, 2) delay “8” & “right hand”, 3) delay “0” & “left hand”, 4) delay “8” & “left hand”. All other manipulations were taken from the first experiment.

Data analysis

Data recording and preprocessing were performed in the same way, as in the first experiment. We also used constant and variable error measures as dependent variables and ANOVAs with the within-subjects factors “delay” (2 levels), “target distance” (8 levels) and “distractor” (intermediate movement: left vs. right hand) for statistical analyzes.
Additionally, we compared the amplitude of the intermediate movements across experimental conditions by using a further ANOVA including all of the above mentioned factors.
In order to investigate the relation between the amplitude of the “encoding” and intermediate movements, we computed Spearman’s Product Moment Correlation Coefficients between the target distance and the amplitude of the intermediate movements. Moreover, we also correlated the intermediate movement distances with the constant error values, in order to estimate the possible influence of distraction on the reproduction. We included single trials within each experimental block in this analysis.

2.3.2 Results

The statistical results of the performed ANOVAs are shown in Table 2-3.

Table 2-3. Results of ANOVAs performed with measures of constant and variable errors as well as with the distance of intermediate movements. *p<.05, **p<.01.

	Constant error			Variable error			Intermediate movement		
Effect	df	F	P	df	F	P	df	F	P
"delay"	1,20	**35.17****	**<.001**	1,20	**21.66****	**<.001**	1,20	**32.15****	**<.001**
"distractor"	1,20	.28	.603	1,20	.12	.733	1,20	**35.95****	**<.001**
"distance"	7,140	**8.50****	**<.001**	3,60	**42.59****	**<.001**	7,140	**54.13****	**<.001**
"delay x distractor"	1,20	**4.91***	**.039**	1,20	.52	.481	1,20	.45	.512
"delay x distance"	7,140	**3.56****	**.007**	3,60	.77	.513	7,140	1.33	.271
"distractor x distance"	7,140	2.13	.084	3,60	.32	.810	7,140	1.73	.148
"delay x distance x distractor"	7,140	.59	.767	3,60	.63	.599	7,140	**2.82****	**.009**

The extension of delay duration was associated with an increase in response variability and a decrease in overshooting tendency (see Figure 2-3 A and C top for means). As the movement distance increased the response variability decreased (Figure 2-3 C bottom). The tendency to overestimate the target distance was reduced in the longer delay condition and this trend increased with target distance (Figure 2-3 A). These results replicated the findings from the first experiment, in which similar time dependent changes were observed.

However, in contrast to the previous results, the manipulation of the "motor distraction" affected the constant error. Intermediate movements executed by the left hand were associated with a larger overshooting error in comparison to the right hand condition, when the delay interval was shorter (see Figure 2-3 A top). This relationship reversed in the longer delay condition.

Although the subjects received the same instruction in all conditions, the amplitude of the interpolated movements varied to some extent dependent on distance, delay and / or distractor manipulation (see Figure 2-3 B for means). The shortest distances were obtained under the delay "0" condition, in which interpolated movements with the left hand had to be performed. The distance increased, when movements were executed with the right hand under the same delay condition and with the left hand under delay "8" condition. As the delay was long and the right hand was used for the intermediate task an additional increase in distance was obtained. The performed statistical analysis revealed a significant "delay x distance x distractor" interaction indicating that mentioned differences were also dependent on distance condition. As can be seen in Figure 2-3 (B), an increase in target distance caused an increase in the amplitude of intermediate movement, which varied to some extent dependent on the delay and the distractor condition.

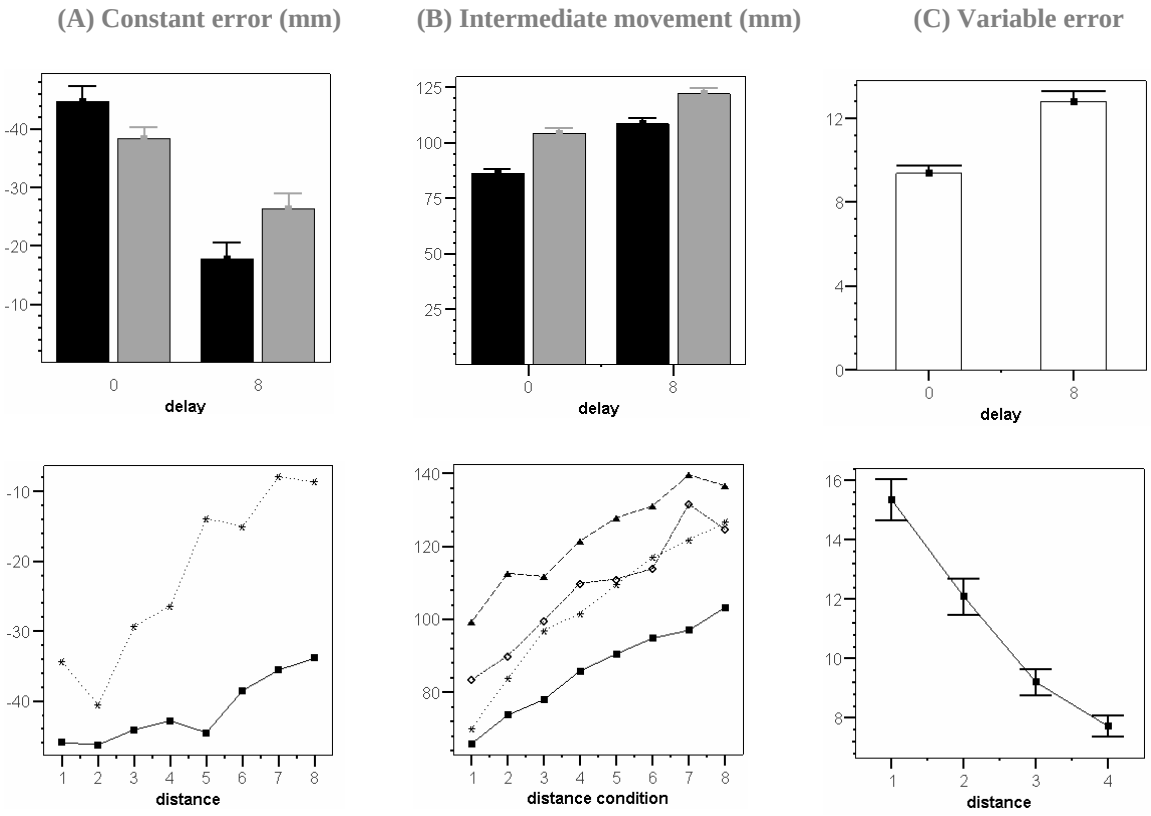

Figure 2-3. (A) Mean constant error values as function of delay and distractor (top), or distance (bottom) conditions (Intermediate movement: ■ - left hand, □ - right hand; Delay: —■— short delay, ···✳··· long delay). (B) Mean amplitude of the distractor movements (Top: ■ - "left hand", □ - "right hand"; Bottom: —■— "short delay & left hand", ···✳··· "short delay & right hand", --◇-- "long delay & left hand", -▲-. "long delay & right hand". (C) Mean coefficients of variability as function of delay duration (top) and distance condition (bottom). Note: two neighboring distances were treated as one in this analysis (see Methods of Experiment 1).

In order to detect possible effects of the encoded distance on the magnitude of the distractor movements, we calculated correlation coefficients between distances of the first ("encoding") and interpolated movements. Moreover, we correlated the amplitudes of the interpolated movements with the constant error values. Figure 2-4 illustrates the results of these analyses. All correlation coefficients of the first analysis (encoding movement & interpolated movement) were significant indicating that interpolated movements were affected by the distance moved previously (all Ps<.001). However, only when the interpolated movement was performed with the left hand under the delay "0" condition and with the right hand under the delay "8" condition, its amplitude significantly predicted the constant error occurring during reproduction. This result indicates the amplitude of the reproduction movement was affected by the distractor movement only under these two conditions.

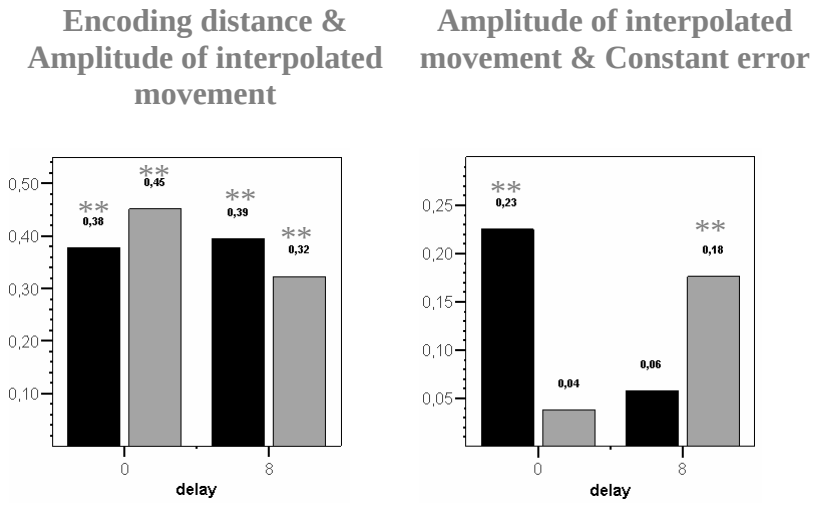

Figure 2-4. *Left*: Correlation between target distance and the amplitude of the interpolated movement (the negative sign was omitted). *Right*: Correlation between the amplitude of interpolated movements and the constant error values. Note: the black bars indicate the experimental conditions, in which the left hand was used for distractor movements, while gray bars correspond to "right" hand conditions. Significant correlation coefficients are marked - *p<.05, **p<.01.

2.3.3 Discussion

The delay and the distance manipulations affected the constant and the variable error measures in a similar way, as in the previous experiment. The response variability increased with an increase in delay duration and with a decrease in target distance, presumably indicating a decay of information with time, and the changes of memory trace stability associated with distance specific encoding efficiency (see Experiment 1 for discussion). The detected shift of the constant error in the direction of "undershooting" was also evident in the first experiment ("empty interval effect") as well as its distance specific characteristics.

The interpolated motor activity only affected the constant error. This result confirmed early observations, in which the variable error increased only, when the interpolated movement had to be remembered (Laabs & Simmons, 1981). This fact was used as an argument for the independence of biases from processing capacity. Moreover, the effect of the interpolated movement was highly dependent on the delay condition. Under the immediate response condition, the subjects overestimated target distance stronger, when they used their left hand for the intermediate task, as compared with conditions, in which the right hand was used. In contrast, when the delay was longer, an opposite effect occurred.

Unfortunately, the length of interpolated movements also varied dependent on the delay and distractor manipulation. However, these differences alone can not explain the observed delay

dependent changes of the constant error (see upper part of Figure 2-3, A and B). When the interpolated movement was performed with the right hand, the subjects covered longer distances in both delay conditions. The constant error by contrast, showed an inverse relation of both distractor conditions dependent on the delay duration. Thus, even considering the results conservatively, one would argue for differences between both distractor conditions being present at least under one of the two delay conditions.

By asking the subjects to produce an additional movement with different hands, we intended to investigate the nature of representation which is maintained and used for the planning of movements towards kinesthetically defined targets. More precisely, according to findings suggesting a critical role of initial effector specific representations under short delay conditions within somatosensory modality (Harris et al, 2001), we expected differences between both distractor conditions when the retention interval was short. Interpolated movements performed with the same hand were assumed to stronger affect reproduction movements as the interpolated movements with the left hand. In longer delay conditions we did not predict any changes.

Contrary to these assumptions, we detected significant effects of the distractor manipulation on the constant error measures under both delay conditions. Moreover, the amplitude of the interpolated movements increased with an increase in target distance under all delay and distractor conditions. This result resembles “assimilation effects”, reflecting constant error changes in the direction of prior stimulation, which were often obtained in several early motor memory studies (Laabs & Simmons, 1981). There is evidence that an increase in difference between interpolation and standard leads to an increase in assimilation effects (Trumbo, Milone, & Noble, 1972). Thus, in respect to the distance manipulation in the given experiment, one would expect that an increase in distance during encoding will produce an increase in movement amplitude during interpolation due to a decrease in assimilation. Since the mean distances covered by the intermediate movements were to a great extent shorter as the mean target and reproduction distances, such “anchor effects” should also occur between intermediate and reproduction movements (i.e. biases towards “underestimation” may account for the reproduction).

Considering only the mean constant error values averaged over all distances according to the distractor and delay conditions (Figure 2-3 A), one may argue for stronger assimilation effects and thus, for stronger interference effects in the “delay 0 & right hand” and “delay 8 & left hand” conditions as compared with both others. However, the amplitude of interpolated movements was higher, when the right hand was used and the delay duration was 8 seconds,

as compared with the “left hand & delay 8” condition. Hence, a pure amplitude difference between right and left hand conditions may be to account for the differences detected in constant error measures under the long delay condition (because a short intermediate movement can be assumed to produce a stronger assimilation affect as compared with a longer movement as previously mentioned). If this is the case, then the constant error results may be interpreted in terms of our hypothesis, suggesting the central role of initial effector specific kinesthetic information in short delay conditions and an involvement of a more abstract representation under long delay conditions.

On the other hand, the performed correlation analyzes indicated a more complex picture. Conditions, which may be proposed to produce stronger interference effects (“delay 0 & right hand” and “delay 8 & left hand”), did not predict the constant error values significantly, while two others did. Moreover, the effect of delay manipulation on correlations between the amplitude of “encoding” and the amplitude of the interpolated movements was expressed in a decrease in correlations with delay, when the right hand was used for interpolation and in a rather unchanged relation, when the left hand was used.

Thus, the processes taking place under given experimental conditions seem to be more complex as initially assumed. A possible reason for these patterns may be derived from recent findings relating to hemispherical specialization in the context of motor control. According to a current hypothesis (“dynamic dominance hypothesis”) the left hemisphere is essentially involved in the control of rather dynamic aspects of behavior (e.g. control of limb trajectory), while the right hemisphere regulates rather static features like limb position and posture (for a recent review see Serrien, Ivry, & Swinnen, 2006). Evidence for this hypothesis comes from studies comparing movement kinematics of both hands among others (e.g. Sainburg & Schaefer, 2004). Following this assumption, one may assume that interpolated movements, which are performed with different hands, may affect the maintenance and planning processes in different ways. Right hand movements would primarily affect some dynamic features of initial representation, while movements performed with the opposite hand should distort some static characteristics like position or posture information.

A decrease in overestimation under the “delay 0 & right hand” condition as compared to the “delay 0 & left hand” condition can be then ascribed to an interference between initial *dynamic* kinesthetic representation and *dynamic* features of the interpolated motor activity when the right hand is used. In contrast, some static parameters associated with intermediate movements performed with the left hand would affect the initial representations to a lesser extent. When the delay interval is prolonged, the relevant representation may be rather *static*

and thus, may be rather distorted by static features associated with the interpolated activity performed with the left hand. Moreover, a decrease in correlations between the “encoding” and the “intermediate” amplitudes with the delay duration in the “right hand” conditions seems to support the mentioned proposals, possibly indicating a decreasing influence of dynamic information in the memory trace. These conclusions would be in line with early motor memory work suggesting that static location cues are superior to dynamic distance information, when information has to be retained over a delay interval of seconds.

None the less, the accomplishment of the results relating to the correlations between the amplitude of the interpolated movements and constant error values are not easy to make congruent with the last mentioned findings and interpretations.

Following early findings indicating selective effects of dynamic and static cues of interpolation on the reproduction of distances and locations (see e.g. Smyth, 1984), we speculate that the interpolated movements performed with the right hand may primarily affect dynamic aspects of the reproduction (e.g. movement duration) and correspondingly, the amplitude of the interpolated movement would not necessarily predict the movement distance of reproduction (see also Experiment 3). In contrast, if rather static features are controlled by the non-dominant arm system, then the static aspect of the intermediate movement may serve as an “anchor” and thereby would better predict the reproduction distance. However, the relation of both movement types (interpolation & reproduction) under the long delay condition can still not be explained.

In spite of this, these results suggest that the distractor manipulation affected the reproduction not only under the short, but also under the long delay condition.

In summary, the results of the present experiment strongly suggest that maintenance and / or planning processes may change dependent on the delay duration. These changes may be associated with the use of different information sources (e.g. dynamic vs. static) and / or with different kinds of handling of the same information (e.g. sensorimotor vs. cognitive modes).

2.4 Experiment 3: “Position vs. Distance”

2.4.1 Methods

Subjects

The current experiment was performed on eighteen right handed volunteers, who received course credit for participating. The data of three subjects were not analyzable due to technical reasons. One further participant was excluded from the analysis because of a large number of artifacts as a result of difficulties in the handling of experimental apparatus. Thus, the data of 14 subjects (5 males and 9 females) between 18 and 26 years (mean age 20) were analyzed.

Paradigm and task

In contrast to the previous experiments, the described apparatus was modified. In the present study we only used six target positions, which were integrated in the device in distances between 13 and 28 cm from the starting position (3 cm between neighboring targets). Moreover, we implemented a change of the initial starting position after the first backward movement by an additional lift magnet that was mounted at 9 cm distance and was activated after the beginning of the first movement. The times were adjusted so that the first forward movement was not obstructed and the first backward movement was stopped at the new position. The subjects were asked to reproduce either the given *target position* or the *covered distance* from the new start location. Additionally, the delay duration was manipulated in the same way as in the two previous experiments (“0” vs. “8”). Again, the experiment was performed block by block (“0” & “distance”, “0” & ”position”, “8” & “distance”, “8” & ”position”) by using a repetition factor of 8 (i.e. each target was presented 8 times in each experimental block).

Data analysis

As in all previous experiments, we used an ultrasound motion device (ZEBRIS, CMS 20) to record movement trajectories of the manipulandum. In addition to the estimations of movement end positions, which were used for constant and variable error measures, we computed tangential velocity and acceleration by using standard differentiation techniques in

the current study. Maximal velocity and acceleration values of the reproduction movements were determined for each trial.

Thus, we defined constant error, variable error, peak acceleration and peak deceleration as dependent measures and analyzed them statistically by using repeated measures analyzes of variance (ANOVAs) with “target distance” (6 levels), “delay” (2 levels) and “reproduction mode” (2 levels: “distance” vs. “position”) as within-subjects factors.

There is evidence that some features of a movement are preplanned and that early kinematic parameters, like peak acceleration, can be considered as a signature for such planning processes (e.g. Gordon and Ghez, 1987a and b, Messier and Kalaska, 1999). Based on these findings, we computed Pearson’s correlation coefficients between peak acceleration and movement amplitude, as well as between peak acceleration and movement duration. These analyses may allow conclusions, whether rather some “static” features like end position or movement distance, or rather dynamic parameters like movement time serve as control parameters during reproduction. The correlations were calculated on the single trial basis for each subject and each experimental block (“delay 0” & “distance reproduction”, “delay 8” & “distance reproduction”, “delay 0” & “position reproduction”, “delay 8” & “position reproduction”).

2.4.2 Results

Table 2-4 shows the results of performed ANOVAs on the constant and variable error values.

Table 2-4. Statistical results of two ANOVAs, computed for the constant and variable error measures.

	Constant error			Variable error		
Effect	df	F	P	df	F	P
“delay”	1,13	4.65	.05	1,13	**19.40****	**.001**
“reproduction mode”	1,13	1.72	.212	1,13	**13.81****	**.003**
“distance”	5,65	**22.75****	**<.001**	5,65	**50.95****	**<.001**
“delay x reproduction mode”	1,13	1.10	.314	1,13	**7.17***	**.019**
“delay x distance”	5,65	**11.35****	**<.001**	5,65	1.24	.299
“reproduction mode x distance”	5,65	**4.91****	**.001**	5,65	**8.84****	**<.001**
“delay x distance x reproduction mode”	5,65	1.59	.176	5,65	.74	.537

The constant error was affected by the delay and distance manipulation in a similar way as in the two previously reported experiments. As the target distance increased, the overshooting

bias decreased and the delay influence increased (the delay dependent drift towards less overestimation increased with target distance (see Figure 2-5 A).

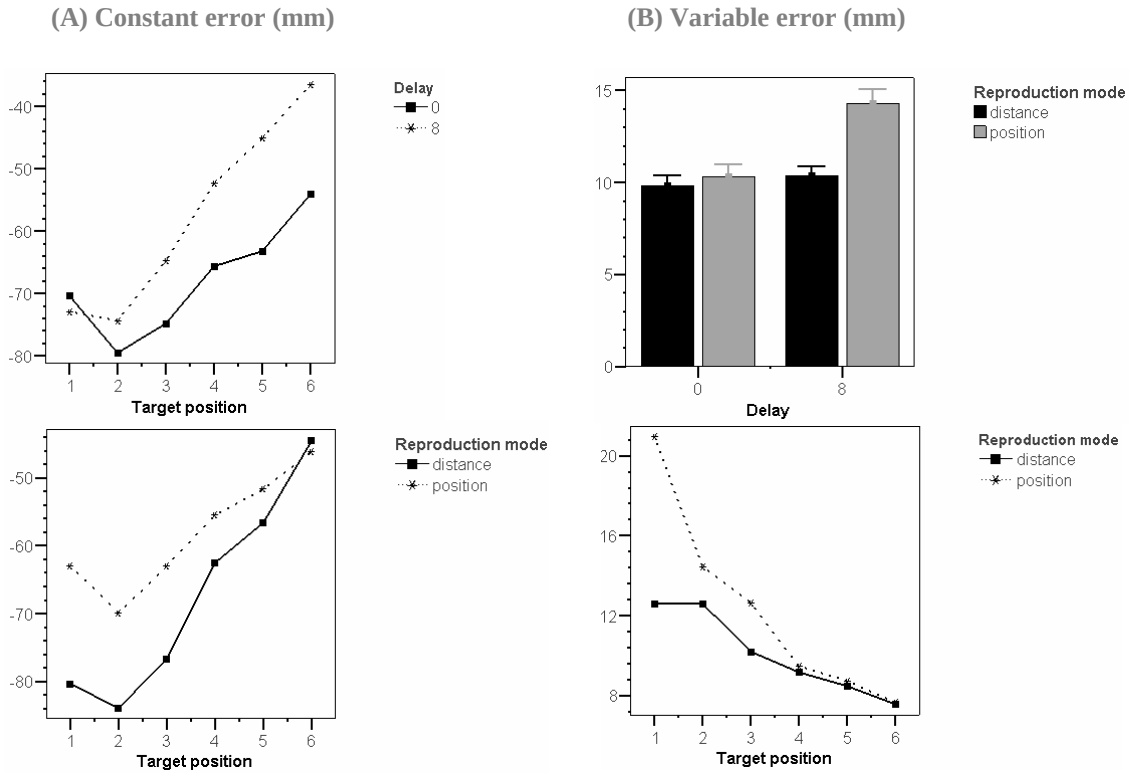

Figure 2-5. Mean values of constant and variable error measures averaged according to the statistical results.

The response variability, as indicated by the used coefficient of variability, was comparable for both response modes (position and distance reproduction) under the short delay condition as well as in the distance condition under the longer delay duration. However, when delay was prolonged, reproduction of target position was associated with an increase in variability (see Table 2-4 for statistical results and Figure 2-5 B for means). Thus, the delay manipulation affected only the position reproduction in the current experiment. Moreover, a decrease in variability with target distance was obtained in both response mode conditions. However, differences across eight targets were more pronounced, when position reproduction was required, as compared to the distance reproduction (Figure 2-5 B).

Position, velocity and acceleration profiles of the manipulandum recorded in one single trial are depicted in Figure 2-6.

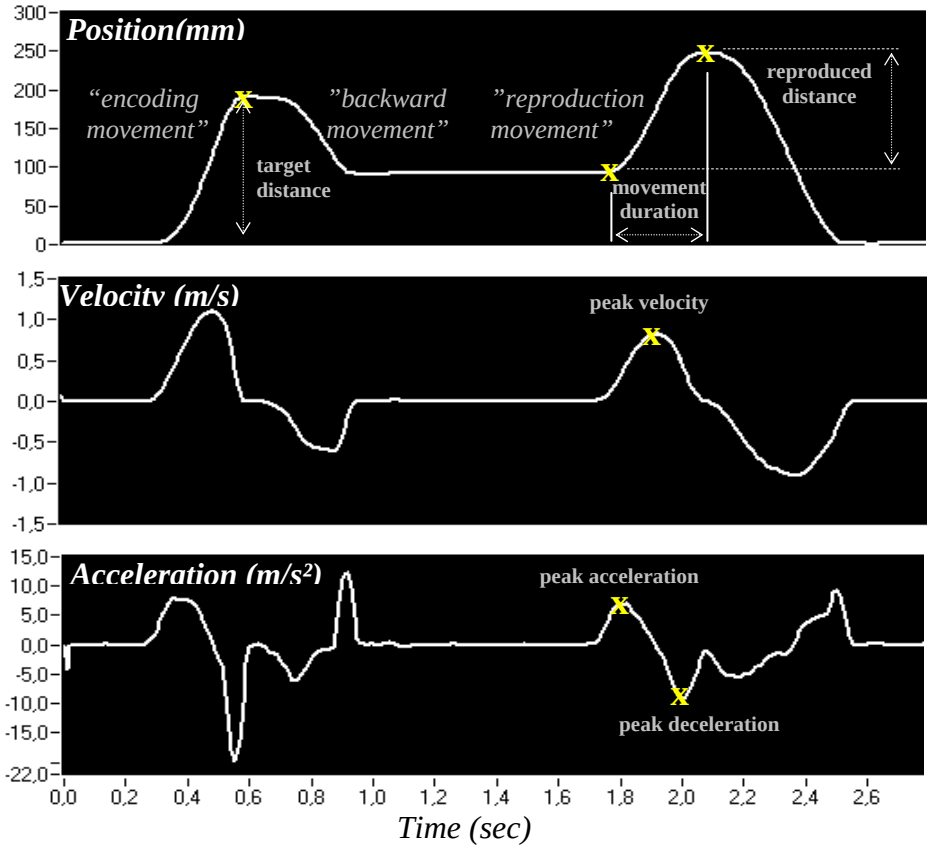

Figure 2-6. Position, velocity and acceleration trajectories of the manipulandum in a single trial. Marked position indicate values chosen for analyses. Note: the time scale is synchronized to the first imperative Go-signal.

Movement kinematics of the reproduction movements had usual characteristics like single-peaked bell-shaped velocity profiles, biphasic acceleration and approximately linear position courses. However, for the "encoding movement" the velocity trajectory was often not bell-shaped, due to mechanical breaking and the corresponding acceleration course had an atypical form (see Figure 2-6).

Figure 2-7 shows the distance specific changes of acceleration of the first forward movement ("encoding movement"). As shown, the peak acceleration does not scale with target distance, while maximal deceleration values decreased with movement distance. This unusual picture is a result of the test arrangement. The subjects were blindfolded and did not know where the movement would be stopped. Thus, they should have preplanned a default trajectory. Since the acceleration trajectory became more "natural" with an increase in target distance, we assume that a far position was initially aimed.

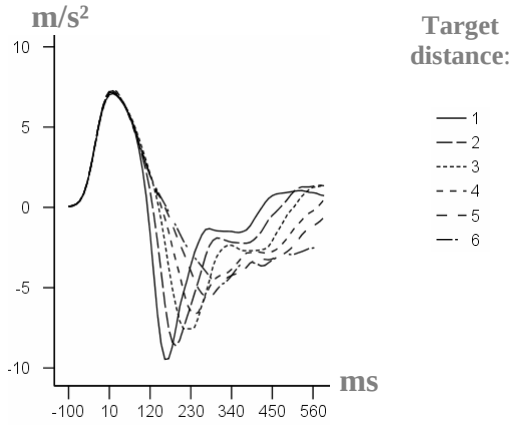

Figure 2-7. Mean acceleration profiles of encoding movements stopped at six target distances and synchronized to movement onset as defined in the method section (averaged over all subjects).

The averaged kinematics of the reproduction movements illustrates Figure 2-8. Visual data inspection revealed that position, velocity and acceleration scaled with target distance under all delay and response mode conditions. However, when the task was to reproduce the target distance, the maximal acceleration shows less pronounced distance differences as compared with position reproduction (See Figure 2-9 for means). Moreover, peak deceleration was modulated in a similar way as during encoding, when the subjects reproduced the target distance (see Figure 2-9 for means). An increase in target distance caused a decrease in maximal deceleration. In contrast, in the position conditions an opposite trend was observed. We statistically analyzed effects of experimental manipulations on peak acceleration and peak deceleration. The corresponding results are shown in Table 2-5.

Table 2-5. Result of ANOVAs performed with maximal acceleration and deceleration values (within subject factors: "delay" (2), "distance" (6) and "reproduction mode" (2).

	Peak acceleration			Peak deceleration		
Effect	df	F	P	df	F	P
"delay"	1,13	**37.13****	**<.001**	1,13	**24.33****	**<.001**
"reproduction mode"	1,13	1.96	.185	1,13	.25	.628
"distance"	5,65	**23.66****	**<.001**	5,65	1.54	.190
"delay x reproduction mode"	1,13	.72	.411	1,13	.00	.985
"delay x distance"	5,65	1.07	.384	5,65	2.91	.052
"reproduction mode x distance"	5,65	**3.87****	**.004**	5,65	**8.74****	**<.001**
"delay x distance x reproduction mode"	5,65	.37	.870	5,65	1.47	.213

An increase in delay duration was associated with a decrease in peak acceleration and deceleration, as indicated by significant main effects "delay". The significant "reproduction mode x distance" interactions suggested, furthermore, that the scaling of analyzed values with target distance was different, dependent on whether distance or position was reproduced. As mentioned above, these effects arose from a stronger scaling of peak acceleration during

position reproduction compared with the distance reproduction, and from an opposite distance specific scaling of peak deceleration dependent on reproduction task.

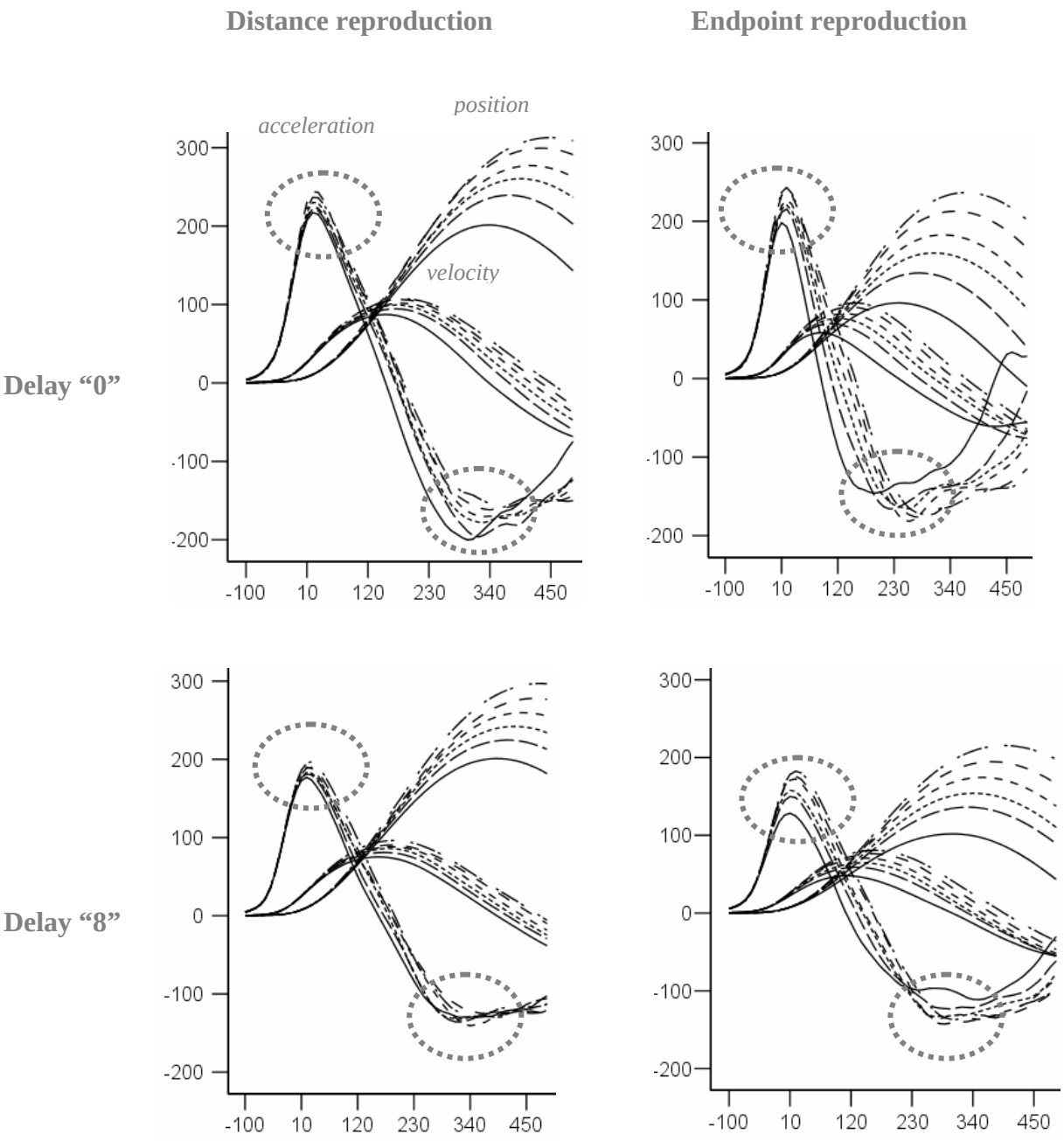

Figure 2-8. Position, velocity and acceleration trajectories. Each line represents kinematic parameters according to one target position averaged over all subjects with follow line assignment: 1 2 3 4 5 6 . X-scale corresponds to time in ms in respect to movement onsets as defined in the method section. Values of the Y-scale are mm (for position), 100 x m/s (for velocity) and 30 x m/s² (for acceleration).

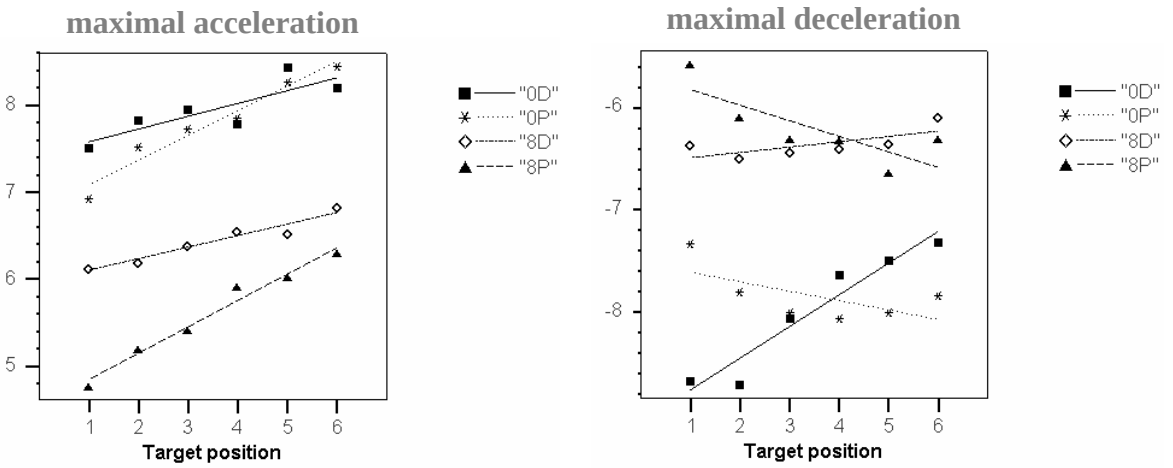

Figure 2-9. Maximal acceleration and deceleration values according to all experimental conditions (D = distance reproduction, P = position reproduction, “0” and “8” stand for both delay conditions)

In order to get further insights into motor control processes, which take place in the given task situation, we computed correlation coefficients between peak acceleration and movement distance and duration (see methods). Figure 2-10 shows the mean values from this analysis.

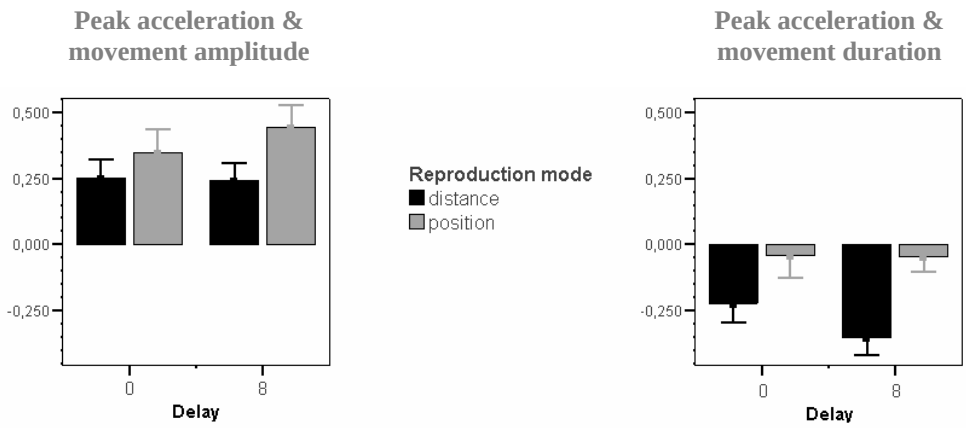

Figure 2-10. Mean correlation coefficients between peak acceleration and the amplitude of the reproduction movement as well as between peak acceleration and movement duration during reproduction. Calculations based on individual subjects data (single trials) from four experimental blocks (distance & “0”, distance & “8”, position & “0”, position & “8”, i.e. including all target positions).

The performed analysis of variance (ANOVA) indicated that there were significant differences between both reproduction mode conditions (see Table 2-6). When the subjects reproduced the movement distance, peak acceleration better predicted the movement duration as when target position was reproduced. In contrast, the amplitude of the reproduction movement correlated stronger with peak acceleration under “position” condition as compared with the “distance” reproduction.

Table 2-6. Statistical results of ANOVAs performed with individual correlation coefficients between peak acceleration and movement amplitude, and between peak acceleration and movement duration.

	Peak acceleration & movement amplitude			**Peak acceleration & movement duration**		
Effect	df	F	P	df	F	P
"delay"	1,13	.20	.664	1,13	.79	.391
"reproduction mode"	1,13	**6.59***	**.023**	1,13	**22.52****	**<.001**
"delay x reproduction mode"	1,13	.87	.369	1,13	1.61	.226

2.4.3 Discussion

The results of the current experiment were comparable in respect to the delay and distance specific changes of constant error measures as well as to the influence of the distance manipulation on response variability to those obtained in the two previous experiments (for discussion see Experiment 1).

Additionally, we detected a somewhat different distribution of biases across six distance conditions dependent on whether distance or stop position was reproduced. The reproduction of the covered distance was associated with stronger overshooting in near distance conditions, as compared with the position reproduction. As distance increased the difference between both response modes decreased. The obtained different slopes of both response mode conditions may be referred to "assimilation" processes described in the previous experiment, which were extensively investigated by Walsh, Russell, Imanaka, and James (1979) in situations where the starting position was systematically varied. The authors demonstrated that the reproduction of movement distance is inferred with by the end location of the encoding movement and conversely, the reproduction of movement location is inferred with by encoding distance (e.g. the subjects overestimated the distance when the starting position was moved away from the original location and they underestimated the target location in the same situation).

In the present experiment the new starting location was identical for both response mode conditions. According to the results of Walsh et al., we can expect that position reproduction would be biased in the direction of overestimation and this effect would increase with an increase in target distance. On the contrary, the distance reproduction should be affected in the direction of underestimation and this effect should also increase with an increase in target distance. Thus, two opposite trends (to greater over- vs. under-shooting) with an increase in target distance would explain the different slopes of both response mode conditions.

A similar, but an inverse relation was obtained while analyzing the response variability. Under both response conditions the coefficient of variability decreased with the target distance. However, when subjects reproduced terminal locations, the slope of this decrease was steeper as compared with distance reproduction. We assume that this effect may be related to different control strategies applied under both conditions (see also below). We speculate that under the given experimental situation a recoding of dynamic information from an encoding movement could be less influenced by the conflict between afferent and efferent signals described in the first experiment, as an extraction of static locations. On the other hand, the mentioned effect may also reflect a somewhat different discriminability according to Weber's law, due to the different length of reproduction movements performed under both response conditions (see e.g. Laabs & Simmons, 1981).

The main purpose of the present experiment was to investigate the motor memory performance dependent on delay duration and mode of reproduction. According to several findings from motor memory research (see e.g. Laabs & Simmons, 1981), we expected similar results of distance and location reproduction under the short delay condition, and an advantage of location cues over distance cues under the long delay condition. In line with this hypothesis, we obtained no differences between the response variability of location and distance reproduction, when the delay was short. This result conformed early observations (e.g. Hagman, 1978, Hagman & Francis, 1975) and indicated that dynamic kinesthetic cues can be used at least as well as static location information for immediate reproduction. Contrary to our assumption as well as to several early reports, the location reproduction was associated with a higher response variability as compared to distance reproduction, when the delay was long. There may be several reasons for this unexpected pattern. We used a coefficient of variability that reflects a relative measure of response consistency being independent from the amplitude of movement. Since dependent measures were and are quite inconsistently used (see e.g. Laszlo, 1992), the discrepancy may be simply related to the different dependent variables. In order to test this hypothesis, we also analyzed standard deviations of reproduction movements and variability of constant error values (computed analog to the coefficient used in the present study). In fact, both measures revealed higher values under both delay conditions when the subjects reproduced the distance as compared with location reproduction. However, due to the different length of movements performed in both responses conditions, we assume that the used coefficient of variability is the most appropriate measure in the given experiment.

Furthermore, the task was quite unusual (rapid movements along the mid-saggital axis, displacement of starting position in the direction of movements) and may also make it difficult to compare our results with others.

The visual inspection of movement kinematics during “encoding” confirmed our assumption that the subjects performed the first forward movement aiming at a far position (see also Experiment 1). Mechanical movement breaking caused the acceleration profiles to adopt a quite unusual course with a decrease in maximal deceleration values with target distance. Moreover, when the subjects were asked to reproduce the covered distance, the acceleration profiles had the tendency to be quite similar to those obtained during “encoding”: the maximal acceleration values only differed slightly across target conditions and peak deceleration decreased with target distance. On the contrary, when the task was to reproduce the current stop position, a stronger scaling of peak acceleration (an increase with an increase in movement distance) and a trend towards an increase in peak deceleration was obtained. These differences were independent from the delay manipulation suggesting that both response mode conditions were associated with specific control strategies, which were applied under both delay conditions. Moreover, when the subjects reproduced the covered distance, they obviously followed the “unnatural” spatiotemporal characteristics of the “encoding” movement. Unlike the distance reproduction, movements to terminal locations were associated with a usual scaling of acceleration that is often obtained in movements to visual targets (see e.g. Messier & Kalaska, 1999, Gordon, Ghilardi, Cooper, & Ghez, 1994).

By analyzing kinematics of monotonic flexion force impulses at the elbow in conditions, in which the subjects tried to match the amplitude of a visually presented target, Gordon and Ghez (1987 a and b) obtained that initial peaks of the second time derivative of force (d^2F/dt^2) were highly predictive of the peak force achieved. Based on this result, the authors suggested that the peak d^2F/dt^2 can be used as an operational measure of the preprogrammed scaling of responses. When reaching movements to memorized visual targets were investigated, a strong association between early kinematic parameters, like peak acceleration or peak velocity and movement distance was also reported (e.g. Messier & Kalaska, 1999). Additionally, both of these findings revealed indices that movement duration (or control of movement time) may also serve as a control variable during movement execution.

Following these results and in order to examine the kinematic characteristics of distance and position reproduction, we correlated peak acceleration with movement duration and with movement distance. When the subjects were asked to reproduce the stop position, the peak acceleration predicted better the movement extent as compared with the distance

reproduction. Conversely, the relation of movement time to peak acceleration was stronger pronounced, when the task comprised the distance reproduction compared with the reproduction of stop location. According to these results, we may assume that subjects controlled rather dynamic parameters under distance reproduction condition (e.g. movement duration), while position reproduction was rather associated with the control of static features (e.g. end position or posture).

Summing up, we ascertained quite different kinematic features of movements associated with distance and position reproduction, which appeared to be differently related to the control of static and dynamic characteristics. When reproduction was required immediately, movement variability was comparable in both reproduction conditions, suggesting that both, dynamic and static cues can be used reliably for reproduction. However, under the long delay condition, the location reproduction was less consistent as distance reproduction possibly indicating a benefit of dynamic information over static in the given experiment.

2.5 Experiment 4: “Forgetting in the milliseconds range”

2.5.1 Methods

Subjects

Nineteen right handed subjects participated in the present experiment. The data of sixteen subjects had sufficient quality and, thus, were analyzed. This final sample comprised six men and ten women between 19 and 32 years (mean age 25).

Paradigm and task

In the present study we used eight target locations again, which were arranged at distances between 14 and 35 cm from the starting position (3 cm between neighboring locations). The task consisted of a simple reproduction of stop positions achieved by encoding movements. The essential manipulation referred to the time variation between two imperative GO-signals (i.e. delay duration), which we aimed to adjust to five intervals. They were to contain 0, 200, 400, 600 and 800 ms between the end of the first backward movement and the acoustic Go-signal indicating reproduction movements. Based on the results from a pilot experiment, we used the time variation according to Table 2-7.

Table 2-7. Times (in sec) between two acoustic signals indicating encoding and reproduction movements.

		Target distance							
		1	2	3	4	5	6	7	8
Delay condition	0	1.038	1.104	1.170	1.236	1.302	1.368	1.434	1.500
	200	1.238	1.304	1.370	1.436	1.502	1.568	1.634	1.700
	400	1.438	1.504	1.570	1.636	1.702	1.768	1.834	1.900
	600	1.638	1.704	1.770	1.836	1.902	1.968	2.034	2.100
	800	1.838	1.904	1.970	2.036	2.102	2.168	2.234	2.300

We used a repetition factor of 16 in this experiment (i.e. each distance was presented 16 times in each delay condition). The experiment was divided into ten blocks, in which the delay duration was held constant. The order of blocks and distances was randomized.

Data analysis

As dependent variables we used constant and variable error measures, like in all of the experiments reported up to now. In the last experiment (3), peak deceleration proved to be

essential in dissociation of distance and end position reproduction. Thus, we measured peak deceleration additionally, in order to investigate the effect of the delay duration on this kinematic parameter. All three variables were put to the analysis of variance (ANOVAs) including “delay” and “distance” as within subject factors.

2.5.2 Results

Table 2-8 summarizes the statistical results according to the analysis of variance for peak deceleration, constant and variable error measures.

Table 2-8. Main effects and interaction of performed ANOVAs.

	Constant error			Variable error			Peak deceleration		
Effect	df	F	P	df	F	P	df	F	P
“delay”	4,60	**3.36***	**.015**	4,60	**10.10****	**<.001**	4,60	1.44	.250
“distance”	7,105	**28.68****	**<.001**	7,105	**86.15****	**<.001**	7,105	**14.51****	**<.001**
“delay x distance”	28,420	1.51	.154	28,420	**2.44***	**.016**	28,420	.85	.540

An increase in target distance was expressed in a decrease in response variability and in a change of response biases following an obvious nonlinear function, which also tended to be the result in the previous experiments (see Figure 2-11 A, middle part and B, right). The significant “delay x distance” interaction in the analysis of response variability indicated that the mentioned effect was dependent on the delay duration to some extent (see Figure 2-11 A, right).

An increase in delay was generally associated with an increase in response variability and a decrease in overestimation. However, these changes seem to not be monotonic. As shown in Figure 2-11 (A and B), an initial increase in variability and a decrease in constant error until 400 ms is followed by a slight decrease in variability and an increase in constant error at 600 ms. Post hoc comparisons indicated that the mean constant error of “600ms” condition differed significantly from those of “400ms” (P = .036) and “800ms” (P = .025) conditions. Similarly, the mean response variability at “600ms” decreased significantly in respect to the “400ms” condition (P = .035) and marginally significant in respect to the “800ms” condition (P = .098). The “delay x distance” interaction in case of variability analysis was significant indicating delay dependent distance differences. However, the last mentioned “break” seems to be present in all distance conditions (see Figure 2-11 A).

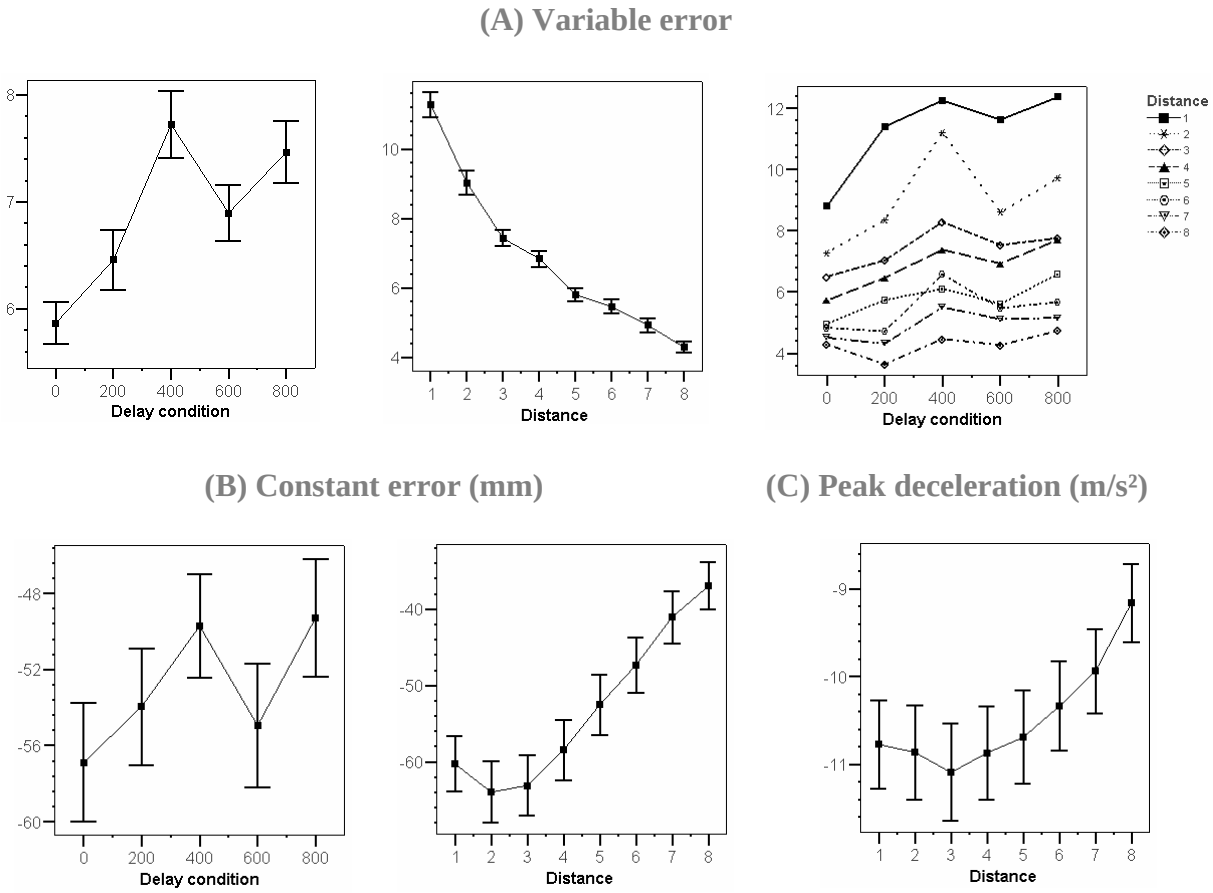

Figure 2-11. Mean values of dependent measures averaged according to the statistical results.

Maximal deceleration values were only affected by the distance manipulation. They showed a similar modulation as the constant error (see Figure 2-11 C). Apart from the two nearest target positions, the mean peak deceleration decreased with target distance. This pattern was obtained in all delay conditions (see Figure 2-12) and was similar to the results of the "distance conditions" from the previously reported experiment (Experiment 3).

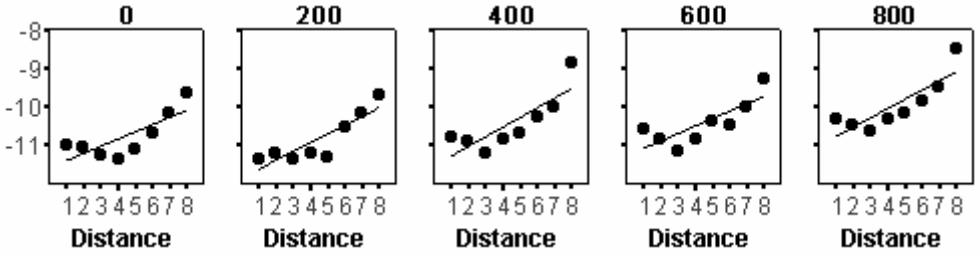

Figure 2-12. Mean deceleration values under five delay conditions (m/s²)

2.5.3 Discussion

By investigating the variability and the biases of reproduction movements in the current experiment, we replicated some basic results obtained in all of the previous experiments. The response variability decreased with the target distance, probably indicating an improvement in memory associated with different amounts of conflict between afferent and efferent signals during encoding (see Experiment 1 for discussion). The constant error was also similarly modulated by the distance manipulation as in the previous experiments. We also referred this result to the assumed informational discrepancy during encoding (see Experiment 1).
Moreover, in the first two experiments we detected an increase in the response variability (see Figures 2-1 A and 2-3 C) and a distance specific decrease in constant error with an increase in delay (Figure 2-1B and Figure 2-3 A). In contrast to the last mentioned finding, we did not observe a significant interaction between “distance” and “delay” factors in the present study. This fact may indicate that processes leading to the different slopes of constant error distributions obtained under two delay conditions in the previous experiments, took place after a delay of “800”ms (see Experiment 5).
However, the shift of biases in the direction of “underestimation” (“empty interval effect”) was already evident in the milliseconds range. It was characterized by a continuous course until “400” ms, an abrupt increase in overestimation when delay was “600”ms and a further shift in the direction of underestimation at the “800”ms delay. Moreover, an increase in response variability followed a quite similar course: an initial increase until “400”ms was followed by a slight decrease under “600” ms and a further increase in the “800”ms condition.
Since the pioneer work of Ebbinghaus (1985/1964), there has been much attempt to describe the effect of time on the retention of information. Several studies replicated his basic finding, indicating a smooth, monotonic, decreasing at first, but then leveling course of forgetting. This characteristic proved to be appropriate for data from a wide range of retention intervals, for different dependent measures, for different procedures as well as for different species (see e.g. Rubin and Wenzel, 1996, White, 2001, Wixted, 2004 for reviews).
According to this evidence, our results appear to be rather unexpected. Especially the obvious increase in memory performance, as indicated by the used measure of the response variability, from “400” to “600” ms delay conditions contradicts any intuitive assumptions. Our post hoc explanation of this effect is depicted schematically in Figure 2-13.

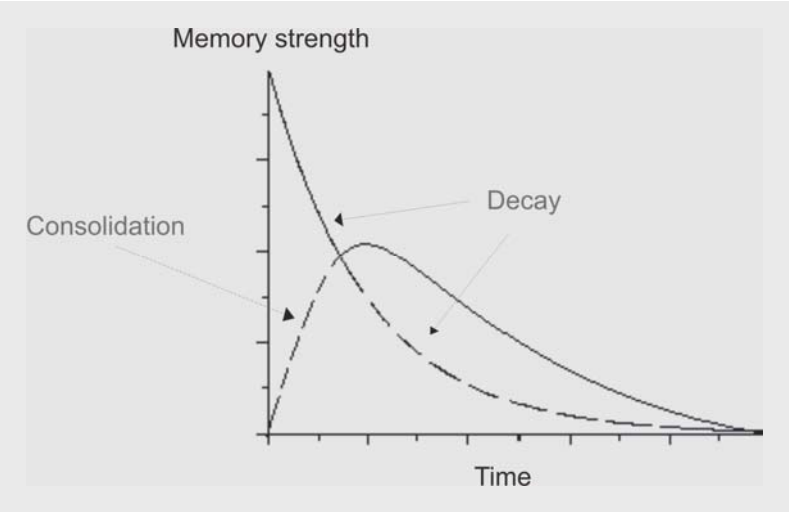

Figure 2-13. Assumed processes leading to the observed changes of response variability and biases in the current experiment.

We propose that the retention of relevant information in the investigated time window may rely on two different functional systems with different retention characteristics (e.g. with different forgetting rates). The fading (decay) of information within one of them may be "compensated" by a downstream one that may enable retention over a wider time range. After a certain delay, one of the assumed mechanisms may provide a more "stable" information source for at least a short time.

Although this proposal seems to be highly speculative at first, we detected several indices from the literature speaking for its plausibility:

1. The retention functions are not always monotonic (Sargisson & White, 2001, see also White, 2001, for a review). White (2001) reported results from delayed matching-to-sample studies with nonhuman animals indicating that the performance level at one delay can be independent of whether performance at a shorter delay is higher or lower. Experiments, in which reinforces were omitted at different delays, showed that under some conditions, accuracy at later delays can be higher than at shorter (e.g. when animals were not reinforced for correct responses at the 2 sec delay, their performance dropped, but only in this delay condition, leading to an increase in accuracy at the 4 sec interval. By varying the delay in the seconds range in simple pointing tasks, Rossetti and colleagues (see Rossetti & Pisella, 2002 for review) obtained constant and variable error courses, which obviously followed a "two-step function". The performance increased drastically between 0 and 1 second and remained relatively stable for longer delays. However, between 1 and 2 seconds the mean variable error

and the mean constant error slightly decreased (see e.g. Fig. 4.11 in Rossetti & Pisella, 2002) and showed a further slow increase after 2 seconds. A similar non-monotonic time dependent course of movement variability is reported by Wolpert et al. (1995). The subjects were asked to localize the end position of their hand, which was previously moved. Until the movement times of approximately 1.2 seconds, the response variability increased rapidly. The slightly longer durations (until approximately 1.6 sec) were associated with a slight decrease in variability. A further increase in movement time caused a further slow-growing drift towards more variability.

2. There is evidence that the shape of forgetting can differ dependent on the time range of analysis. By analyzing the recognition memory for pitch in a delayed comparison task, Wickelgren (1969) argued for two memory traces (short-term and intermediate-term), which showed decay at different rates. Similarly, based on results from several further studies, Wickelgren (1974) emphasized different dynamics of retention processes on different time scales (exponential decay within the short-term memory, “exponential power” decay within the long-term memory), which were taken as argument for dissociation of short-term from long-term memory mechanisms among others. Moreover, the author suggested a decrease in the rate of decay with an increase in time range. By reanalyzing the results from early studies, in which short-term memory of letter or word trigrams (seconds range) and long-term memory for campus locations (years) were investigated (Peterson & Peterson, 1959, Murdock, 1961, Bahrick, 1983), Wickens (1998) showed that the failure of an exponential function to fit the long-term retention performance (LTM) (as opposite to STM) may arise from a retention dynamic, in the course of which the retention rate may change (decrease). These differences were referred to possible consolidation and competition processes taking place within the LTM. Rubin, Hinton and Wenzel (1999) demonstrated further that a function containing two exponential terms with different time constants predicts a wide range of data. The first term with a short time constant was referred to the working memory according to Baddeley’s model, while the second term was considered as the description of a long-term or of an intermediate and a long-term memory process.

3. As mentioned by Wixted (2004), “consolidation” as a progressive stabilization of long-term memory, was only rarely discussed within the traditional experimental psychology. In contrast, in neuroscience its important role has been recognized for a long time. The main idea within this research domain is that new memories initially persist in a fragile state and, thus, need time to stabilize (see e.g. Dudai, 2004, McGaugh, 2000 for reviews). Moreover, recent findings suggest, that consolidation may occur in parallel on different “hierarchical” levels (e.g. “synaptic” (seconds to minutes and hours) vs. “system” (weeks, month, years) consolidation, “long-term” (hours to months) vs. “long-lasting” (months to lifetime) memories). In line with these findings, Jolicoer and Dell’Acqua (2002, see also Jolicoeur, Tombu, Oriet, & Stevanovski, 2002) reported evidence for the existence of consolidation processes within a short time range. This phenomenon was called “short-term consolidation” and referred to the process of the encoding information from perceptual representations, which were assumed to decay rapidly, into a more stable short-term memory. There are several further lines of evidence for consolidation processes in the range of milliseconds and seconds in the visual modality (Jiang, 2004, Potter, 1976, Chun & Potter, 1995, Raymond, Shapiro, & Arnell, 1992, Vogel & Luck, 2002, Vogel, Woodman, & Luck, 2006, Ward, Duncan, & Shapiro, 1996).

4. The time of the assumed “switching” is comparable with the “typical” duration of the early sensory memory (~ few hundreds milliseconds, see e.g. Pashler & Carrier, 1996, see also Bliss, Crane, Mansfield, & Townsend, 1966 for evidence of tactile sensory store similar to the iconic memory) as well as with the time range of early consolidation processes (e.g. Chun & Potter, 1995, Jiang, 2004, Jolicoeur & Dell’Acqua, 1998, Ward et al., 1996)

These results suggest that information can be maintained within different functional and / or neuronal systems, which may have different dynamics (2,3). Although we cannot derive statements about forgetting / retention rates from the recent results, due to a sparse number of intervals, the assumption that a “later” system may forget slower is in agreement with findings reported in 2. Moreover, some needed “consolidation” processes may also be expected within a short time range (milliseconds or seconds) and may give rise to an increase in memory performance in respect to a previous time point (3).

The monotonicity of functions is, furthermore, not a necessary result of the delay manipulation and may disappear in certain recall conditions (1, see also Wickens, 1998). As mentioned, we assume that the deviation from a typical monotonic form in the present study may arise from a change of access to relevant information. Since the latency of the “break” is comparable with the duration of classical sensory memory store (4), the “switch” from such an early retention system to a more durable storage appears to be appropriate.

It is worth mentioning that several other parameters like peak velocity, peak acceleration and reaction times were affected by the delay manipulation in a similar manner as the constant and the variable error measures.

Based on the results from the previous experiment, we also measured peak deceleration in the current study. The distribution of mean peak values of deceleration across eight target conditions resembled the result patterns obtained in the third experiment under the “distance reproduction” condition. Apart from the first two target locations, the peak deceleration decreased with target distance. The resulting “non-linearity” may arise from a different number of distance conditions (6 vs. 8) and / or from the manipulation of the starting position used in the third experiment. None the less, the current result suggests that the subjects used similar control strategies in both of the mentioned task situations and followed an “unusual” deceleration characteristic of the encoding movement, rather than to extract a “static” position. This trend was evident in all delay conditions used in the present experiment.

2.6 Experiment 5: "Forgetting in the seconds range"

2.6.1 Methods

Subjects

Subjects were twelve right handed students of the University of Marburg. The data from three participants were excluded from further analyses due to a large number of artifacts. The remaining nine subjects were seven females and two males between 21 and 28 years (mean age 23).

Paradigm and task

The task, as well as the apparatus, were the same as in the previous experiment. The subjects were asked to reproduce a given stop position after a varying delay interval. In the current experiment we aimed to investigate the influence of time in the range of seconds on motor memory performance. Thus, we used six delays of "0", "1", "2", "4","6" and "8" seconds[4]. The experiment consisted of six blocks corresponding to six delay conditions, in which each target distance was presented three times.

Data analysis

All data analyzes were performed in the same way as in the previous experiment except for the variability analysis, in which two neighboring target positions were considered as one, as in Experiments 1 and 2.

2.6.2 Results

Statistical results according to the performed ANOVAs on mean peak deceleration, constant and variable error values are shown in Table 2-9.

Table 2-9. Main effects and interactions of ANOVAs applied to the peak deceleration, constant and variable error measures.

	Constant error			Variable error			Peak deceleration		
Effect	df	F	P	df	F	P	df	F	P
"delay"	5,40	.67	.547	5,40	1,65	.196	5,40	2.08	.155
"distance"	7,56	**19.93****	**<.001**	3,24	**41.41****	**<.001**	7,56	**8.76***	**.002**
"delay x distance"	35,280	**2.81***	**.021**	15,120	.86	.517	35,280	**2.51***	**.039**

[4] Note: these intervals do not correspond exactly to the real delay times, since like in all the previous experiments the time between two imperative Go-signals was manipulated based on pilot experiments.

The response variability was only affected by the distance manipulation. As in the previous experiments, an increase in distance was associated with a decrease in variable error (see Figure 2-14 for means). The overestimation biases were dependent on distance and delay manipulation. As delay increased, the subjects showed the tendency to overshoot the first four target positions stronger and to overshoot the distant four target positions to a lesser extent. Moreover, the results appear to suggest that the biases tended to approximate a middle target range (between positions 4 and 5) in longer delay conditions, since the overestimation seemed to increase from the first to the fourth target and to decrease from the fifth to the eighth target conditions (see Figure 2-14 B).

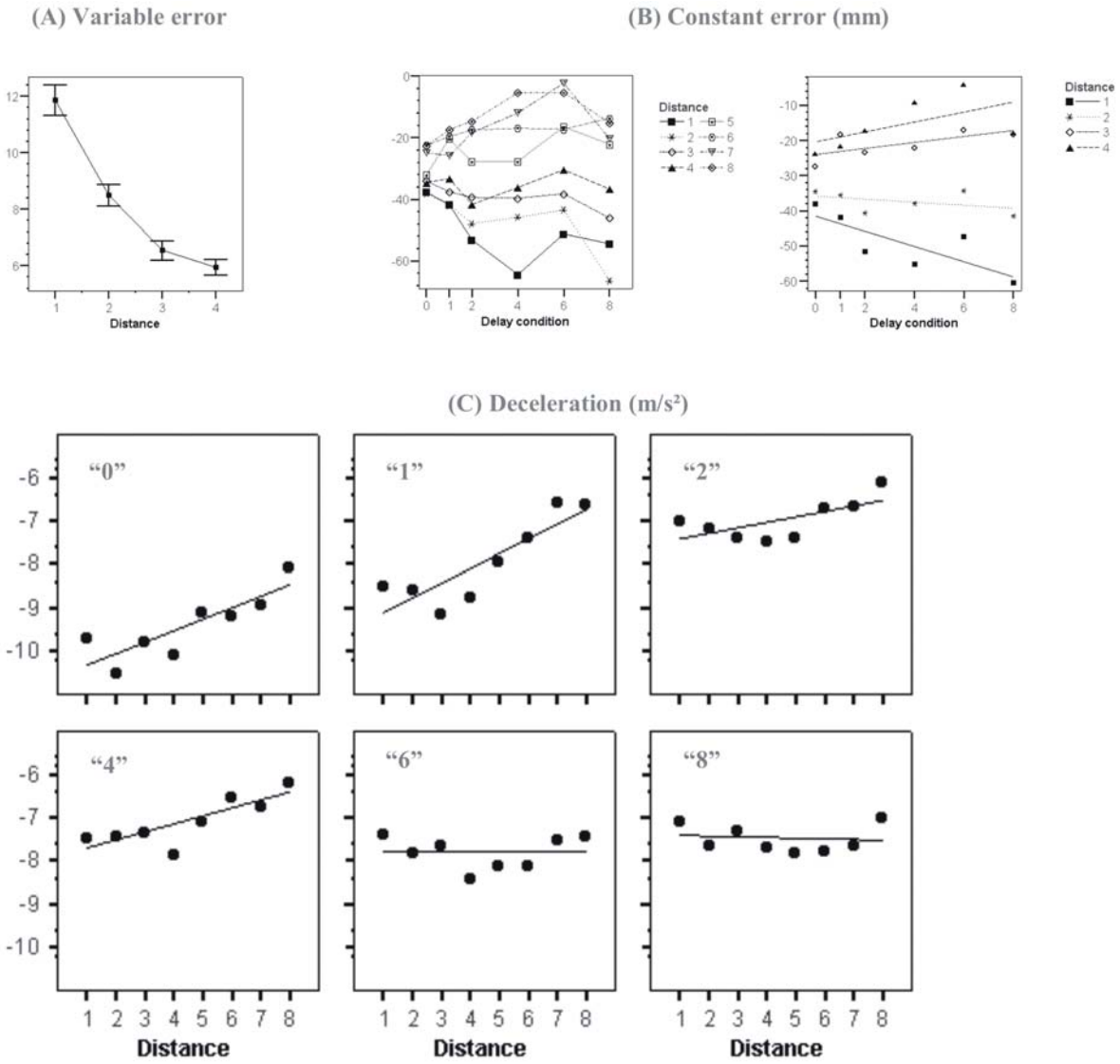

Figure 2-14. Mean values of peak deceleration, constant and variable error values averaged according to the statistical analyzes. Note: for descriptive purpose, the constant errors are also shown as function of two neighboring target distances (B, right) with regression lines indicating the course of delay dependent changes.

Peak deceleration values were spread across eight target positions in the two shortest delay conditions similarly, as in all delay condition of the previous experiment (and as in the "distance" condition of the third experiment). An increase in movement distance caused a tendency to decrease the maximal deceleration. However, when the delay interval was extended beyond one second, the effect of distance manipulation on peak deceleration seemed to decrease and to approximate the results pattern, obtained in the position conditions of the third experiment.

2.6.3 Discussion

The coefficient of variability decreased with target distance, confirming our prior results. Although a trend towards a decrease in response consistency with longer delay was obtained, the corresponding main effect did not reach the significance threshold. This somewhat deviant result in comparison with prior experiments (1,2,4) may arise from a rather small repetition factor and / or a rather small subject sample. Despite a low power, the constant error results as well peak deceleration patterns revealed a consistent picture, as expressed in significant effects of variance analyzes.

In line with the experiments 1 and 2 and in contrast to the experiment 4, we found a significant "delay x distance" interaction, which suggested significant changes of distance specific biases dependent on the delay duration. When the delay was short ("0" or "1" seconds), there were only slight trends towards "less overshooting" with an increase in distance (~20mm between two extreme distances). However, in longer delay conditions a strong increase in discriminability was obtained (e.g. ~ 59mm between two extreme distances under "4" seconds delay). Moreover, by considering the shortest delay condition as a kind of "baseline", longer delays would be associated with an increase in overestimation at four nearest distances and a decrease in overestimation at farther distances.

In many perceptual judgments as well as in motor memory experiments, in which a small set of stimuli along the same dimension was presented several times, similar effects often occurred (e.g. Smyth, 1984, Laabs & Simmons, 1981). In such experimental situations, the subjects tend to overestimate small stimulus intensities and to underestimate large stimulus intensities. There is also some evidence that these "range" or "central tendency effects" may increase over comparison intervals and may replace or obscure the usual "empty interval effect" (for review see Laabs & Simmons, 1981). In the context of motor memory, the range

effect was assumed to depend only indirectly upon the memory decay. Instead, it referred to an influence of contextual information. According to Laabs (1973, see also Laabs & Simmons, 1981) the range effect occurs, when a sensory memory trace of a prior movement decays and the “adaptation level” (mean level of a given set of movements) becomes more important (i.e. a weighting of contextual information increases with delay, while the influence of sensory information decreases). This hypothesis would explain why no central tendency effects were obtained in the previous experiment, in which short delays were used (for comparable results from the visuomotor domain see e.g. Westwood et al., 2001).

From a more general point of view, the constant error results from the two last experiments seem to suggest that information about a given context (range of target positions) enters in the processing only after a certain delay interval (>1sec). If so, then the performance of a given task under longer delay conditions would be associated with the involvement of “more abstract” information as compared with short delay conditions, in which the reproduction would rely mainly on the sensory memory trace.

The analysis of peak deceleration in the current experiment revealed results, which appear to be in line with the previously mentioned assumptions. Under the short delay conditions (“0” and “1”) we obtained a similar “unusual” distance specific scaling as in the previous experiment as well as in experiment 3 under the “distance reproduction” condition. As the distance got larger, the peak deceleration decreased. When the retention interval was extended to one second, the slopes indicating distance differences became flatter and reached a negative value in the longest delay condition. Thus, we may assume again that when the retention interval was short, the subjects rather followed the “unnatural” dynamic of the “encoding” movement during the deceleration phase. However, from about two seconds the patterns of peak deceleration seemed to deviate gradually from those, obtained under both the shortest delay conditions and successively to approximate the results patterns obtained in experiment 3 under the position reproduction condition. This result seems to suggest that the relevant information used for the planning of the reproduction movement, became more “static” with an increase in delay.

Furthermore, the delay dependent changes of the constant error distributions, obtained in the two distractor experiments as well as in the third experiment, may now be explained with the combination of the two well-known effects. The “empty interval effect” leads to a decrease in overestimation und seems to already take place early after the “encoding” movement, while the “range effect” appears to be pronounced at longer delays and to change the slope of biases distributions across eight target conditions.

Finally, in the previous experiment (4) we identified a rather non-monotonic course of error measures dependent on delay duration, which we referred to as possible changes of processing characteristics. Interestingly, we also obtained a similar picture in the current study by analyzing the response variability (the corresponding result was not shown since we did not detect significant delay effects) and the reaction times (not reported). Figure 2-15 shows these results. Except for a high variability of data, the mean values of both measures rather follow a “two-step” function (or two functions) than one with a monotonic course. As already mentioned, such patterns are not unusual and may indicate further changes in the processing between 2 and 4 seconds, if our assumptions are correct (see 5.3).

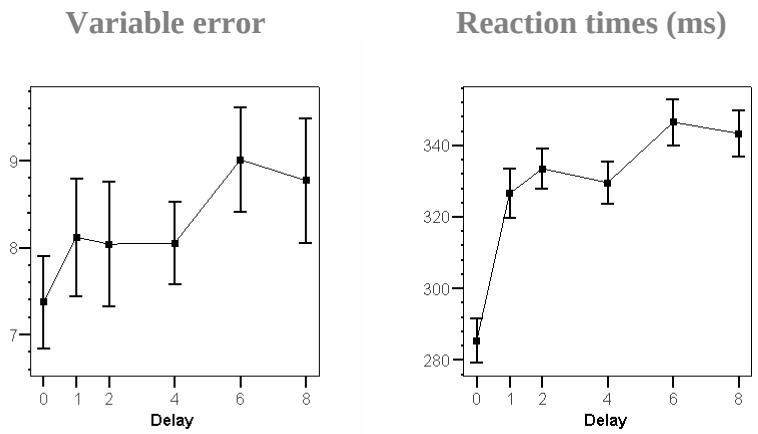

Figure 2-15. The mean variable errors and mean reaction times averaged over all distance conditions as function of the delay duration (in sec). Note: error bars represent standard error values; reaction times are defined as the time between the reproduction tone and the time, when movement amplitude exceeded 5 mm.

2.7 General discussion

The main goal of the experiments was to investigate the role of delay duration on the memory of spatial locations, which were defined kinesthetically.

The results of the first experiment indicated that the verbal judgments of target distance affected the motor reproduction only, when the retention interval was long (“8” sec). A detected increase in response variability as compared with the “unfilled” condition suggested that the maintenance of relevant information over the range of several seconds required attentional resources. Since no effects of verbal judgments on the movement amplitude of reproduction were found, we concluded that information sources used for motor planning and for verbal judgments were independent from each other. Moreover, by following the results from motor memory research, indicating an advantage of location cues over dynamic distance information, we assumed that the critical representation used for motor planning during the longer delay condition, may rather be static and possibly extrinsic. On the contrary, the lack of interference in the short delay condition may suggest a rather kinesthetic source of information (e.g. dynamic distance information).

This interpretation seems to be confirmed by the results of the second experiment, in which short interpolated movements with the right vs. left hand were performed between the encoding and the reproduction phases. The duration of the retention interval and thus, the time of the interpolation proved to be critical for the influence of the implemented distraction. Higher overestimation biases were obtained, when subjects performed intermediate movements with their left hand as compared to the right hand condition under a short delay duration. By contrast, when the delay was long, an inverse relation was evident. Although the results from this experiment only allowed restricted statements, due to a lack of an “unfilled” condition among others, the proposed distinction of using different information sources (dynamic vs. static) could explain the main patterns to a large extent.

In the next experiment (3) we aimed to investigate the delay influence on the retention of static vs. dynamic information directly. According to early motor memory studies, we asked the subjects to reproduce the location of the stop vs. the covered distance from a new starting position. In agreement with our hypothesis, we obtained no differences in respect to the response variability when the delay was short. This result indicates that both information types may reliably be used for motor planning if a response is required immediately. Moreover, we detected the rather different kinematics of reproduction movements dependent on whether location or movement distance had to be reproduced. Distance specific changes of

acceleration profiles resembled the “untypical” course differences during the encoding movement, when the distance was reproduced. The location reproduction, in contrast, was associated with acceleration scaling often obtained in unrestricted movements to visual targets. The performed correlation analyzes suggested further that dependent on response mode either dynamic or static control parameters were used during reproduction.

In the two last experiments we varied the delay duration in the milliseconds (Experiment 4) and in the seconds range (Experiment 5). We found a similar distance specific scaling of peak deceleration, as obtained in experiment 3 under distance reproduction condition, when short retention intervals were used (until approximately 1 second). From about 2 seconds the results appeared to deviate from this untypical pattern and to approximate those of position reproduction in experiment 3. Thus, the subjects obviously followed the rather unnatural dynamic of the encoding phase during maximal deceleration, when the delay was short, and began to “correct” this only after about 2 seconds delay. These results may be considered again as evidence for changes in access to different information sources (dynamic vs. static). This hypothesis seems further on to be supported by the constant error results. The “range” effect indicating an influence of context (target range) did not occur in the milliseconds range, but was evident in the longer delay conditions.

Thus, our results as a whole suggest that the time of response may play an essential role for sensorimotor processes taking place in similar task situations. Although some conclusions may not be compelling, the bulk of detected indices seems to indicate that sensorimotor transformation processes occurred within an “intrapersonal” space (i.e. kinesthetic parameters of encoding movements were directly used for the reproduction), when the response delay was short: the reproduction was unaffected by verbal judgments, but was affected stronger by interpolated movements performed with the right hand than with the left hand, no range effect and a similar scaling of peak deceleration as during encoding was obtained. In contrast, under longer delay conditions verbal judgments affected the response variability, left hand interpolation obviously caused more interference as right hand interpolation, range effect was pronounced, scaling of peak deceleration changed in the direction of the position reproduction. These results indicate that the relevant representation was more abstract and rather static, suggesting an involvement of extrinsic processes (i.e. initial kinesthetic representation was transformed in a spatial one before or during motor planning). These conclusions seem to confirm early observations as well as more recent findings. In early motor memory experiments retention intervals of several seconds were usually used (from 10 to 45 seconds, see Laszlo, 1992). As mentioned, the majority of these results indicated a

benefit of static location information over dynamic distance coding. This fact was referred to a possibility of a more abstract coding of location (e.g. in a spatial frame). Rosenbaum et al. (1999) suggested an alternative interpretation based on their results, using however a rather short delay (about 1 second). According to this, location information would be maintained in an intrinsic frame (as end posture). In contrast, Baud-Bovy and Viviani (1998, 2004) implemented longer retention durations (about 3 and 4 seconds from target onset) and argued again for planning in an extrinsic frame of reference. The subjects in the studies of Tillery et al. (1991, 1994) obviously reproduced immediately (exact times are not reported). The authors favored the intrinsic scheme over a spatial one. Adamovich et al. (1998) reported evidence for both types of processing by using a delay between 1 and 2 seconds.

Moreover, our results also do not appear to contradict the “dual mode approaches” mentioned in the introduction. One may argue that intrinsic computations are rather “direct” and occur within “the proprioceptive field of postural body space” (e.g. Paillard , 1991a). In contrast, an extraction of extrinsic target coordinates would rather be related to “an internal representation of environmental space” (see e.g. Paillard, 1987). As emphasized by Rossetti and Pisella (2002), both processing modes may be considered as complementary, whose relative dominance may depend on the time between stimulus and response.

However, the whole patterns of our findings can not be fully reconciled with only two “qualitatively” different processing modes. Instead, the current results as well as some other indices from the literature seem to suggest a more complex picture.

By analyzing the movement errors in the milliseconds range (Exp. 4), we identified their non-monotonic course, which we referred to as a possible “switching mechanism” from an early sensory memory to a more durable storage. We also obtained a similar pattern in our last experiment that may indicate a further “temporal marker” in the range of 2 seconds. Moreover, peak deceleration began to deviate from the “untypical” form in a similar time range, while no changes were detectible under the 800 and 1000 ms delay conditions. Additionally, the “range effect” seemed to be absent until 1 second, but strongly pronounced from about 4 seconds. Some other observations (not reported) appeared to confirm two changes in processing characteristics. For example, peak velocity decreased strongly from “0” to “2” seconds with a similar “break” between 400 and 600 ms as obtained at constant and variable error measures, and remained widely constant after that.

Harris et al (2001) identified similar patterns in tactile memory tasks, in which retention intervals of a similar range were used. The authors dissociated performance characteristics, obtained at delays less than 1 second, from those obtained at 1 second and 2 second intervals.

Thus, these indices may indicate that the retention of initially the same information and / or the using of this information for motor planning in the range of seconds may pass through at least three different “formats”.
Looking back on the question related to our coffee example, mentioned in the introduction (“What kind of representation does the brain maintain and use for the planning of a motor act in similar situations?”), we would now answer: “this may depend on the time of response”!

2.8 Concluding remarks

Although our results seem to be rather consistent, they should be considered with caution. The test arrangement was quite unusual and further studies are needed to test to what extent they can be generalized. Moreover, in all experiments block designs were used and we do not know whether similar patterns can be expected if randomization would be implemented. We did not consider the backward movements and thus, can not evaluate its possible influence on the results. Furthermore, we used peak deceleration as the dependent variable among others. We also did not include possible effects of delay on efferent information in our discussion (see e.g. Ito et al. 1991 for evidence of delay effects on the retention of efferent information). Nevertheless, we obtained several results which seem to be confirmed by findings from other task situations and thus, may be valid.

3 EEG-Study 1: “Effects of time and distance on the memory of kinesthetically defined spatial locations: an ERP-Study”

3.1 Introduction

If we make a movement toward a position in space in the absence of vision, only motor-related signals are initially available. How can these signals be used to prepare and execute a movement to the same location after a short time period? Although short-term memory for movements has been extensively studied since 1970s (reviews in Smyth, 1984, Laabs & Simons, 1981, Laszlo, 1992), the knowledge about the sensorimotor processes in kinesthetic tasks is still sparse. Much of the early works attempted to identify the nature of information which is stored or encoded after the movement execution and serves as basis for reproduction. In a typical task, known as “linear positioning”, blindfolded subjects moved their hand and arm in a straight line or curve and then tried to reproduce the final position or the moved distance from a new starting point. The results from several studies indicated that spatial location is a more accurate cue for movement reproduction than the distance information, suggesting that locations can be encoded in a more abstract way than the kinesthetic distance information and thus, are more resistant to forgetting (e.g. Smyth, 1984). However, due to several methodical problems, including a non-unique use of dependent measures or delay between criterion and test movements among others, the findings could not reveal a consistent picture (e.g. Laszlo, 1992). As Rosenbaum et al. (1999) noted, the obvious advantage of location information does not necessarily reflect that this static information is represented in an external frame of reference. Instead, the authors favored, based on their results, a body state hypothesis emphasizing the reproduction of final posture and suggesting a possible explanation of early findings. According to this, the final posture cannot be adequately adopted in the distance conditions due to different start positions in the locating and test phases.

This mentioned distinction between “intrinsic” and “extrinsic” information sources proved to be important for the understanding of movement related internal representations and transformations and was consequently investigated in a series of further studies.

By analyzing the ability to reproduce the spatial position of the passively displaced right hand by using the left hand, Tillery et al. (1994) concluded that the sensorimotor transformations in kinesthetically guided tasks occur within the “intrapersonal” space and are different from

processes underlying visuomotor performance, which require an estimation of “extrapersonal” coordinates. In a previous study the same authors reported posture matching as the preferred control strategy in a task, in which the same hand was used for reproduction (Tillery et al., 1991). Adamovich et al. (1998) could, in contrast, identify some indices for both strategies in similar tasks, concluding that the arm angular configuration as well as the arm endpoint location in external space can be remembered. Using a more controlled design, Baud-Bovy and Viviani (1998) tested both alternatives explicitly, labeled them as “target position hypothesis” and “direct mapping hypothesis”. Subject’s left or right index fingers were guided by a robot to one of 27 target locations in the locating phase. After the active backward movement, participants had to reproduce the target position with the right index finger. Due to the strong similarity of constant and variable errors, irrespective of whether the right or left hand was used in the locating phase, the authors argued for an external representation of the target position as central in kinesthetic pointing. Moreover, postural variability during the pointing phase could be explained with the corresponding variability of the locating posture to some extent, leading the authors to believe that postural memory trace is still available during reproduction, having however, no effect on the average pointing position. By analyzing amplitude and direction errors in another experiment, Baud-Bovy and Viviani (2004) extended their findings and summarized them in a model, consisting of three hierarchical levels: a sensorimotor, a perceptual and a motor, which all contribute to the movement reproduction, affecting however, different control aspects and are accordingly expressed in specific types of errors.

These inconsistent and to some extent ambiguous findings show that one important question relating to the kind of information which serves as basis for planning and execution of kinesthetically guided movements, could not be definitively answered. Moreover, there is evidence that in addition to the mentioned static information sources, dynamic characteristics of the locating movement, like its velocity, as well as motor outflow, can enter into the memory trace and subsequently affect the reproduction movement (e.g. Chieffi, Conson, & Carlomagno, 2004, Jones, 1972, Ito, 1991).

Thus, there are several sources of information, which can be derived from proprioceptive input and motor command and can be used for movement control in kinesthetic tasks. From a computational point of view, the CNS combines these sensory and motor signals in an adaptive way in order to enable optimal movement control (for review see Wolpert & Ghahramani, 2000). However, it is widely unknown how several sensory and motor signals exactly interact. In the face of richness and complexity of motor control processes, there can

be several reasons for complex patterns and contradictory results. One possible aspect that may help to simplify the picture to some extent stems from a further line of research focused on sensorimotor interactions.

Many results from this area led several authors to propose two distinct modes of sensorimotor processing. The direct mode, termed as “sensorimotor” (Paillard, 1991a) “pragmatic” (Jeannerod et al., 1995) or “vision for action / how” (Goodale & Milner, 1992) extracts parameters from sensory flow that are primarily relevant for the generation of a corresponding motor behavior. It is assumed to process absolute metrics within an egocentric frame of reference. In contrast, the “representational” mode (labeled as ”semantic”, “cognitive”, “vision for perception” too), enables to build an internal representation by means of binding of stimulus attributes and assumed to operate within an allocentric or an object centered frame of reference. Although some conclusions and predictions, relating to the neuronal substrate or sensitivity in respect to optical illusions for example, could not be verified up to now and are still controversially discussed, there is a considerable body of neurophysiological, neuropsychological and psychophysical evidence for at least a functional dissociation between the two mentioned systems (for reviews see Jeannerod, 1997, Milner & Goodale, 1995; Norman, 2002, Rossetti & Pisella, 2002). Rossetti and Pisella (2002) suggested that the time aspect may be essential for the dissociation of cognitive and sensorimotor functions. In respect to the kinesthetic modality, they reported a series of pointing experiments in which the delay between a first hand movement (passive displacement) and the reproduction was varied. The authors observed delay dependent changes in relation to the endpoint distribution: Immediate reproduction was associated with a variability ellipse that was oriented in the direction of the pointing movement, while delayed movements (after 8 sec.) caused ellipses oriented towards other targets. An impressive finding, interpreted as further evidence for the temporal dissociation of proposed processing modes in the somatosensory modality, is reported by Rossetti (1998). A patient with tactile and proprioceptive deficits on the right side of body as a result of thalamic lesions was able to locate tactile stimuli presented on the right hand by pointing movements with the left index finger above chance level, while according to verbal reports he was unable to perceive the applied stimulation. Similar results were obtained during a kinesthetic task. However, the obvious ability to guide a movement on the basis of unaware information was lost, when the stimulus response interval extended 2 seconds. Comparable results were observed with an agnostic patient who lost the ability to correctly reach and grasp objects after 2 seconds, which she could not describe (Goodale et al., 1994). The existence of brief representations, lasting a few seconds and which can be used for

precise sensorimotor transformations, is supported by several studies in the visuomotor area, indicating that immediate and delayed actions are controlled differently (Hu, Eagleson, & Goodale, 1999, Bridgeman et al. 2000, Bradshow & Watt, 2002, Elliott & Madalena, 1987, Vaillancourt & Russel, 2002).

The idea that the time between a stimulus and a corresponding response can affect the kind of information processing is not new. Cognitive psychologists could identify several systems and subsystems, which are assumed to be responsible to different kinds of information processing on different time scales. In relation to how long information is retained, the distinction between sensory memory, short-term memory and long-term memory was made. Sperling's pilot experiment (1960) showed that a large portion of initial visual information decays within a few hundred milliseconds. This finding could be replicated in numerous studies and became an integral part of several information processing models (e.g. Atkinson & Shiffrin, 1968). Sensory encoding is traditionally associated with parallel processing, operating over several high capacity channels within a modality and transmitting information about basic stimuli attributes, like color or motion in case of the visual modality (for review see e.g. Massaro & Loftus, 1996). These characteristics are typically considered to be in contrast with more "durable storage" ("short-term memory" or "working memory"), retaining information over seconds to minutes with very limited capacity, fragility of representation, involvement of attention resources, categorization processes etc. (for review see e.g. Miyake & Shah, 1999). More recently, a further subdivision within early visual retention processing was made, assuming a transient storage, which takes place between the early sensory and the classical short-term memory (Magnussen et al., 1998, Magnussen & Greenlee, 1999, Magnussen, 2000, Pasternak & Greenlee, 2005, Ruchkin, Grafman, Cameron, & Berndt, 2003). By varying inter-stimulus interval in a series of psychophysical experiments, which involved a delayed discrimination of basic stimulus attributes, like orientation or spatial frequency, Magnussen and Greenlee (1999) reported that the choice reaction times did not change during the first three seconds. The longer delays were associated with a strong increase, indicating an additional process after a few seconds, which was associated with retrieval from short-term memory. These and other similar results led the authors to believe that perceptual on-line and memory representations are functionally and anatomically distinct. Furthermore, they assumed that perceptual storage is a set of parallel feature-selective mechanisms, which has limited capacity and codes basic dimensions of the visual stimulus, while memory representations involve other codes and a different neuronal substrate.

Independent from the suggested interpretations, the results mentioned above indicate the existence of temporal markers within early sensory processing, which can be associated with changes in the kind of representation or processing characteristics. Can these findings be extended to kinesthetic tasks?

Although knowledge about short-term retention mechanisms in other modalities is sparse, there are some indications that early sensory as well as on-line perceptual mechanisms may be comparable in all modalities, possibly following a general principle of information processing (Magnussen, 2000, Massaro & Loftus, 1996, Pasternak and Greenlee, 2005). If so, one may assume that the initial representation of parameters of a locating movement in a typical motor matching task (or of a stimulus in a visuomotor task) may change over time. This proposal would be compatible with a recent neuroscience perspective of sensory-motor interactions, which suggests different hierarchical levels of perception-action integration (e.g. Fuster 2001, 2004).

In a series of pilot experiments we investigated the role of the delay duration in a motor memory task. In the first experiment the blindfolded subjects performed linear hand movements until they reached a mechanical stop. After a delay of approximately 0 or 8 seconds they had to reproduce a given position of the stop by a further movement. We asked the participants to estimate the current distance of the stop by a verbal report during the delay interval in one condition and compared it with an “unfilled” condition. We found that the variability of movement end points in the judgment condition increased in relation to the unfilled condition only if the delay interval was 8 seconds. Moreover, verbal reports were unrelated to the distances of reproduction movements, and judgment errors were also uncorrelated with movement errors. With a similar test arrangement in a further experiment, we asked the subjects to perform a short intermediate movement with the left vs. right hand during the delay period and manipulated the delay duration again (0 vs. 8sec.). We could observe that the length of the delay was essential for the effect of the used distractor (right vs. left hand) on the constant error, as well as on the correlations between intermediate movements and each other. Thus, the results of both experiments indicated that immediate and delayed responses were differently affected by mental and kinesthetic interference. However, the findings could not be fully explained by a dual-mode approach mentioned above (sensorimotor vs. cognitive). Rather, they were compatible with the idea of different representation levels, which can be used by the motor system. In a third experiment, we again manipulated delay and compared distance vs. position reproduction by changing the first start position. Contrary to previous findings, showing memory for position information to be

superior to distance retention, we expected an inverse relationship in the short delay condition. However, this hypothesis could only partly be supported. While no differences in respect to the movement variability in the short delay condition were detected, reproduction of terminal location was associated with an increase in response consistency as compared with the distance reproduction, when the delay was long. In addition, we found that subjects used quite independent from the delay condition a distance specific and position specific strategies, which were expressed in different scaling of peak acceleration and peak deceleration of the reproduction movement.

The goal of the present study was to extend these findings and to provide further insight into the nature of sensorimotor processing characteristics in the absence of vision. We used a one-dimensional linear positioning task, consisting of a locating phase, in which the subjects moved a manipulandum with their right hand until a mechanical stop, and a reproduction phase of the perceived position after a delay period. Two essential manipulations were implemented. Firstly, we were interested in the role of time between the two movements, and therefore adjusted the delay to three intervals, based on our prior results and theoretical considerations mentioned above. Secondly, we used eight target positions, which were arranged along the mid-sagittal axis (in front of participant) in order to vary the distance.

In addition to the behavioral data analysis, we recorded EEG (electroencephalogram), in order to detect electrophysiological markers of processes which are sensitive to distance and delay manipulations. EEG studies of motor control mainly used two paradigms. By asking subjects to press a button at intervals of their own choice, Kornhuber and Deecke (1965) obtained a slowly increasing negative shift at precentral sites preceding the motor response. This negative deflection, labeled as “readiness potential” or “Bereitschaftspotential”, was extensively studied in similar recording situations since its discovery. The second experimental paradigm was introduced by Walter, Cooper, Aldridge, McCallum and Winter (1964), who used a reaction time experiment, in which a first warning stimulus (click) was presented one second before a second imperative signal (flickering light), which the subject had to react to (button press). The authors obtained a slow negative wave during the interval between the warning and the imperative stimuli, which was initially interpreted as “expectancy wave”. Both research lines revealed descriptions of several components, which were associated with specific functions and neuronal sources (for review see Brunia, 1987, Brunia & Van Boxtel, 2000).

Thus, the EEG proved to be a powerful tool in studying the motor processes. However, in our literature research we could not identify studies with a comparable design, in which delay and

/ or movement distance was systematically varied. According to this, we could not formulate exact predictions about specific components or topographies, which should be responsible for the implemented manipulations. The used paradigm shares some features with both mentioned procedures, i.e. motor preparation and execution. Moreover, there are cognitive functions related to maintenance and processing of relevant information. Therefore, we adopted some terms from the established ERP research for a first description and classification of our results.

In summary, the goal of the present experiment was primarily exploratory. By simultaneous analyses of behavior parameters and EEG data, we aimed to identify electrophysiological and behavioral markers of time and distance specific changes in processing characteristics in a motor memory task.

3.2 Materials and methods

3.2.1 Subjects

All participants in this study were right-handed, neurologically normal students of the University of Marburg who were paid or received course credit for their participation. Data of five subjects had to be excluded from the analysis, due to a large number of EEG artifacts. The final sample comprised eight males and ten females between 19 and 28 years (mean age 22).

3.2.2 Paradigm and task

Apparatuses

The subjects were blindfolded and sat in front of a table, which was placed horizontally slightly above the waist. A linear track device was mounted on the table, allowing one dimensional movements of a pen-like, lightly moveable handle along the mid-sagittal axis of the trunk (90°). Eight lift-magnets were integrated in the device in distances between 10 and 31 cm from the starting position (3 cm between successive magnets). The starting position was defined as the nearest possible handle location in relation to the body (approximately 10 cm). At the beginning of each trial subjects positioned the handle at the start position. The head was placed on a headrest, whose height was adjusted individually. Moreover, we used ear protectors in order to minimize noise effects resulting from movement braking and earphones allowing the presentation of acoustic signals.

Experimental procedure and design

A trial started with an auditory warning stimulus (250 Hz) followed after a fixed interval of three seconds by a first imperative GO-signal (2000 Hz). The subjects were instructed to move the manipulandum rapidly until the stop and then immediately backward to the start. After the second Go-signal (2000 Hz) participants had to reproduce the stop position of the first movement as accurately and rapidly as possible. The inter-trial-interval was randomly varied between 3000 and 3350ms. Moreover the participants could not see the apparatus neither before nor during the experiment.

The essential manipulation consisted of the time variation between the two imperative signals (Go1 and Go2). In order to enable a comparability of different distance and delay conditions, we adjusted the time point of the reproduction tone to the duration of the previous movement. The goal of this procedure was to equalize the length of the retention intervals across the 8

distance conditions, i.e. to create similar durations between the end point of the first backward movement and the second Go-signal. Moreover, we were interested in the role of different delay durations and thus, we varied the time additionally, attempting to initiate the reproduction after less than 500ms, around 1000ms and 5000ms.
Based on results from a pilot experiment, we adjusted the timing between two successive GO-signals for each condition according to the values shown in Table 3-1.

Table 3-1. Delay and distance dependent time intervals between the acoustic signals, indicating encoding and reproduction movements (in ms).

Delay condition	*Target location* 1	2	3	4	5	6	7	8
0	1038	1104	1170	1236	1302	1368	1434	1500
1	2038	2104	2170	2236	2302	2368	2434	2500
5	6038	6104	6170	6236	6302	6368	6434	6500

We used 8 locations x 3 delays x 32 repetitions within-participants block-design. The experiment was divided into 12 blocks, each of them consisting of 64 trials (8 locations x 8 movements), which lasted between 8 and 13 minutes depending on the delay condition. The delay period within each block was held constant (i.e. only one row from Table 3-1 was used in each block). Each participant performed three practice blocks including all delay conditions. The order of blocks and of target positions was randomized with the constraints that two consecutive blocks or targets should correspond to different delay durations or target positions and the whole sequence of delay or target positions should be completed before another repetition.

3.2.3 Recording and data pre-processing

Behavioral data

Movement trajectories of the manipulandum were recorded with an ultrasound motion device (ZEBRIS, CMS 20), consisting of a measuring unit with three ultrasonic microphones and an ultrasonic marker positioned on the handle. By measuring the running time of the ultrasonic pulses the system allows to record the absolute 3D position coordinates in real time. The data were sampled at 100 Hz initially and analyzed with a specially written software using LabView codes (National Instruments, Graphical Programming for Instrumentation).

Tangential velocity and acceleration were computed using standard differentiation techniques. The following parameters were calculated[5]:

1. Movement onset (the first time when the position trajectory exceeded 5mm)
2. Movement termination (first maximum of position trajectory; in case of first backward movement we used a first minimum in an adjusted time window)
3. Covered distance (amplitude of the end point position)
4. Movement duration (time difference between movement onset and corresponding offset)
5. Peak velocity (amplitude of maximal velocity)
6. Peak acceleration (amplitude of maximal acceleration)
7. Peak deceleration (amplitude of minimal acceleration)
8. Acceleration duration (time to peak velocity)

Visual inspection was performed on every single trial to ensure a correct determination of markers.

EEG data

The EEG was continuously recorded from 61 AgAgCl electrodes by using a cap with an equidistant positions montage (Easy cap, System Falk Minow, Munich, Germany, Montage No.10, see Appendix 3-A). All scalp electrodes were referenced to the tip of the nose, grounded to the left mastoid and re-referenced offline to the average reference. Ocular artifacts were recorded and monitored with bipolar electrodes, placed vertically from above and below the left eye (vEOG) and horizontally from the outer canthi of both eyes (hEOG). Electrode impedances were kept below 5 kΩ. EEG and EOG were amplified between DC and 100Hz (gain 500) by using two 32-channel amplifiers (SYNAMPS, NeuroScan) and digitalized with a sampling rate of 500 Hz. Aquire software (NeuroScan) was used for the collection and Brainvision Analyzer Software (Brainproducts) for the analysis of data. DC drift was corrected according to the method suggested by Hennighausen, Heil and Rösler (1993). Eye movement artifacts were removed by application of a regression method (Gratton, Coles, & Donchin, 1983), while trials with other artifacts were rejected based on a threshold criterion, allowing a maximum voltage range of 250 µV within a trial segment.

[5] Apart from the end of the first backward movement, all parameters were determined only for both forward movements.

Markers indicating movement onset and termination were imported offline after the behavioral pre-processing stage and included the onset and the end of both forward movements and the end of the first backward movement.

3.2.4 Data analysis

Behavioral parameters

By using repeated measures analyses of variance (ANOVAs) with target distance (8 levels) and delay (3 levels) as factors, we analyzed the following dependent variables:

1. Reaction times (time difference between second Go-signal and movement onset)
2. Variable error (standard deviation of reproduced distances within one condition)
3. Constant error (mean deviation of the reproduction distance from the corresponding encoding distance)
4. Peak velocity
5. Peak acceleration
6. Peak deceleration
7. Acceleration duration (time to peak velocity)

For all analyses statistical significance was tested on an alpha level of 0.05. Degrees of freedom were adjusted according to the method of Geisser and Greenhouse (1958) and a Bonferroni correction was used in case of pair-wise comparisons.

There is evidence that some features of a movement are preplanned and that early kinematic parameters, like peak acceleration, can be considered as a signature for such planning processes (e.g. Gordon and Ghez, 1987a and b, Messier and Kalaska, 1999). Based on these findings, we performed a trial-by-trial correlation analysis in order to test the relation of the static (distance) and the dynamic (duration) parameters of both movements to peak acceleration and peak velocity of the reproduction. For this purpose we computed Pearson's product moment correlation coefficients between the mentioned variables. For practical reasons, we only focused on delay differences. Standard significance tests were used for determination of significant coefficients (H0 : R = 0, H1: R <>0; df = N-2, alpha = .05). For comparison of correlation values, we applied the Fisher Z-transformation:

$$Zf = ½*\ln((1+R)/1-R))$$

The difference of two transformed values was tested with:

$$z = (Zf1-Zf2)/SQRT(1/(N1-3)+1/(N2-3)),$$

and critical z values were defined according to alpha = 0.05.

These analyses may allow conclusions, whether rather some “static” features, like end position or movement distance, or rather dynamic parameters, like movement time, were stored and served as control parameters during reproduction.
In order to compare the mean peak acceleration values within the encoding movement and between the encoding and the reproduction movement, we computed an ANOVA with factors delay (3) and distance (8) of the peak values of the first movement, and an ANOVA with factors distance (8) and kind of movement (2) separately for each delay condition. All analyses were run with SPSS (12.0).

EEG parameters

Due to a lack of comparable studies, from which exact predictions could be derived, we pursued a data driven approach. Starting from an exploratory goal of the study, we defined five processing phases for further analysis: locating movement (LM), processing after the stop (S), delay (D), motor programming (MP) and reproduction movement (RM). The recorded potentials were then adjusted to the respective triggers: the onset of the first movement, the time of the stop, the end of the backward movement, the acoustic signal for the reproduction and the onset of the reproduction movement. In order to draw conclusions about the differences in each time epoch, which cannot be directly attributed to the preceding epoch, we used a baseline correction in the following manner. Apart from the delay phase (D), the baselines were determined as the averaged activity in the –10 to 0 ms interval (corresponding to 5 data points) preceding each trigger. We chose this short period in order to minimize possible influences of the preceding processing stage. This procedure resulted in a relatively exact adjustment of potentials around zero µV at the time point of each trigger, and allowed us to make a statement about the “new” differences arising in the current time window (which may be of course affected by the preceding processes). It is usually recommended to use a longer baseline, which reduces possible noise fluctuations (e.g. Picton et al., 2000). However, in case of a processing splitting, one has to weigh between possible systematic amplitude differences in the baseline period, which could result in artificial carry-over effects after the trigger, and trigger dependent new effects. Moreover, random noise should affect all conditions similarly, resulting at the short baseline in higher variability of used measures. If there are systematic differences between conditions in the period chosen for the baseline correction, they cannot be directly related to noise. Although we cannot completely exclude the influence of noise, we tried to minimize it by using additional baseline independent measures like peak to peak analysis or by using a longer baseline period, if appropriate.

Furthermore, due to the relatively large number of trials in the experiment and by interpreting only the largest differences between conditions, we assume that the essential findings are only minimally contaminated by noise.

In the delay phase (D) we defined the window between –2000 and –1000 ms before the first "Go-Signal" as the baseline period, in order to measure slow potential changes, unaffected by rapid phasic waves.

After averaging and baseline correction, we divided the chosen processing phases into several 50 ms time windows, whose averaged voltage amplitudes were used for statistical analysis. Apart from MP- and D- phase, the first 300 ms after the corresponding trigger entered into this analysis, resulting in 6 time windows in each processing phase.

In order to include the movement onset of the reproduction and because we were not interested in possible early differences related to auditory processing, the range between 100 and 400 ms after the acoustic signal was chosen for the MP-phase. In order to be able to compare the ERPs of delay phase (D), we divided them into three equal segments depending on delay condition that lasted from the end of the backward movement to shortly before the mean signal-onset for the reproduction. This relies on the assumption that the general processing-characteristic has to be comparable due to the identical physical stimulus and similar task requirements (e.g. maintaining of motor information). These segments were in delay "0" condition 3x50ms, in delay "1" 3x380ms and in delay "5" 3x1700ms.

The complete analysis was performed in a hierarchical fashion, including windowed ANOVAs, principal component analysis (PCA) and additional measures (see below).

(1) The goal of the initial statistical analyses was to identify time periods and locations sensitive to implemented experimental manipulations (i.e. "where" and "when" do different distances and delay conditions affect the amplitude of the ERPs?). Univariate repeated measures ANOVAs were conducted on the mean voltage amplitude of each time window by using algorithms generated by the general Linear Models Procedure of the SPSS (12.0). A conventional significance level (.05) was applied and Greenhouse-Geisser epsilons (Geisser & Greenhouse, 1958) were used for correction of the degrees of freedom.

   (a) Firstly, 27 time window specific ANOVAs with the within-subjects factors "distance" (8 levels), "delay" (3 levels) and "electrode" (61 levels, see results and discussion) were performed. This procedure provided "sensitive time windows" for the manipulations, expressed in significant "electrode" x "distance",

"electrode" x "delay", "electrode x distance x delay" or "distance x delay" interactions.

(b) Secondly, electrode specific ANOVAs with the factors "distance" (8) and "delay" (3) were computed only for time windows, where the above-mentioned interactions became significant, providing "sensitive scalp locations" by significant main effects and interactions of both variables. In order to give a complete picture of effects, we plotted the respective significant F values as topographical maps.

(2) In order to reduce the temporal and the spatial dimensionality of data and to focus on the essential processes, we performed a simplified mode of PCA (principal component analysis). The basic idea behind this procedure was to identify topographies and time courses of "theoretical components" underlying the measured activity and to relate them to the experimental conditions. PCA is a widely applied multivariate statistical technique for decomposition of event-related potentials by analyzing variations in a set of variables (Donchin & Heffley, 1978; Chapman & McCrary, 1995; van Boxtel, 1998; Dien & Frishkoff, 2004). One type of PCA is termed "temporal", if the data are organized as waveforms, i.e. the time points are treated as variables and different waveforms (typically including channels, subjects and experimental conditions) are considered as observations in the data (e.g. Dien & Frishkoff, 2004). The second type is the "spatial" PCA, in which the variables are conceptualized as electrode locations, and observations are time points, subjects and experimental conditions (e.g. van Boxtel, 1998). In general, PCA reduces the large number of variables to a set of "components" or "factors", which are weighted linear combinations of the original variables. In case of temporal PCA, the resulting latent components are waveforms, which are expressed by temporal "loadings", representing the contribution of each component to the voltage of each time point. The topography of components is given by the amplitude of their time-invariant "factor scores" at each electrode (e.g. Dien, 1998). The spatial PCA, in contrast, separates electrodes or clusters of electrodes, providing different component "loadings" as invariable potential distributions with variable time courses ("scores"). Thus, both types of analyses provide information about characteristic features of the waveforms which are spread across multiple time points and electrodes (i.e. "components" or "factors"), emphasizing however, different aspects of the variance (temporal vs. spatial; Dien, 1998).

According to the properties mentioned above, a spatial PCA is useful for a temporal comparison of experimental conditions, which are similar in topography, whereas with a temporal PCA conditions with similar dynamics can be topographically analyzed (for similar suggestions see e.g. Dien, 1998, Dien & Frishkoff, 2005). By following this, we performed several PCAs depending on a priori assumptions and prior statistical analysis. In case of different distances we did not expect strong topographical differences, (which was confirmed by visual data inspection), and therefore we treated them as "topographically similar" by using the spatial type of PCA in the time epochs, where we found significant effects in the mean amplitude. In relation to the delay conditions we postulated possible "qualitative" differences, which should be expressed in distinct potential distributions and used temporal PCAs in order to extract the main waveforms and to compare the topographies of experimental conditions in the phases, in which delay effects became significant.

Because of the large amount of data and the relatively modest goal of the procedure, we did not aim at a statistical analysis on the PCA level and therefore only decomposed the grand average signal in space and time. Thus, subject variance was excluded from the analyses. Hence, the basis for the components built in case of the temporal PCAs, the spatial and the task variability (61 electrode sites and 24 experimental conditions), whereas in the spatial PCAs the time points and the conditions served as sources of variance. The solutions represent the waveforms and topographies, which are related to the over all subjects averaged activity. We found a reliable congruency in high variance factors by comparing the results of grand average PCAs with the usual procedure in some selected time periods. Moreover, PCAs were used here in a very conservative way. Since PCA solutions partially depend on used parameter settings as association matrix and rotation technique, we implemented four common settings over each time range – covariance matrix & Varimax rotation, covariance matrix & Promax rotation, correlation matrix & Varimax rotation, correlation matrix & Promax rotation. We followed the suggestions of Kayser and Tenke (2005; Kayser & Tenke, 2003) and extracted the maximum number of components ("unrestricted" solutions), but interpreted only the high variance factors.

In the results section we present only covariance-based and Promax-rotated solutions. According to this, all units of the component scores and loadings are in µV (van Boxtel, 1998; Chapman & McCrary, 1995). Since the results provide relative variance measures,

the polarity of them is arbitrary[6] (Donchin and Heffley, 1978; van Boxtel, 1998; Dien & Frishkoff, 2004). The data about the "eigenvalues equal one rule" is derived from the unrotated and correlation based solutions, while details about the scree test and the explained variance stem from covariance data (before rotation). Apart from the MP phase, data input for PCAs consisted of the same time segments chosen for windowed ANOVAs (i.e. 300 ms after the respective trigger at the LM, S, RM phase and from the end of the first movement till the reproduction tone in the D phase). In contrast to the statistical analysis of the raw data, we analyzed for PCA the MP phase in the time range 0-300 ms after the "Go-Signal", in order to focus processing before movement onset. All PCAs were conducted with SPSS (12.0).

(3) Based on the PCA and the statistical results we analyzed some "regions of interest" additionally, by using peak-to-peak- and peak-to-baseline-measures, or considering post hoc comparisons at representative scalp locations in representative time windows. Details of the used procedures are reported in the results section. In case of the analyses of variance (ANOVAs), as well as in the prior analyses, the alpha level for significance was chosen to be .05 and all probabilities of observed F-ratios were adjusted according to the Greenhouse-Geisser method, while all post hoc tests were adjusted for multiple comparisons by using the Bonferroni correction.

(4) In order to localize the essential condition differences, we performed a source analysis based on a priori assumptions, as well as on statistical and PCA analyses in two selected time epochs. If we detected significant differences in the mean amplitude between the conditions, we concluded that these differences must be caused by differences in the activation of the underlying generators. The goal of this analysis was to delineate, whether "quantitative" or "qualitative" factors may have caused the observed differences. Following recommendations (Picton et al. 2000), according to which signals with little noise should enter such computations, we used only the grand average signal of 24 conditions for source estimations. The Low Resolution Tomography method (LORETA, Pascual-Marqui, Michel, & Lehman, 1994, Pascual-Marqui ,1999) was applied, which estimates intracerebral distribution of current density generating the scalp recorded ERPs. Starting from the physiological assumption that neighboring neuronal sources are active synchronously and simultaneously, the LORETA algorithm solves the inverse problem by finding the "smoothest" of all possible activity distributions. The resulting solutions represent the amplitude of current density at each voxel in neuroanatomic Talairach

[6] They reflect variations around grand mean and only the product of loadings and scores represent the original data adequately.

space (µA-equivalent), which is restricted to gray matter and the hippocampus. LORETA does not require assumptions about the number, localization, configuration or extent of neuronal sources, making this technique especially applicable to the present study.

(5) The procedures described so far seemed to be useful due to a lack of comparable results. However, some disadvantages also became apparent. In order to clarify some incurred questions and to provide more detailed information about the electrophysiological markers of the involved processing in the given task, we analyzed evoked activity at selective electrode locations additionally, following a priori theoretical assumptions and the behavioral results. The respective reasons and further details are reported in the results section.

In short, by using statistical analyses, we intended to localize time periods and scalp locations, which showed distance and delay related changes in the mean voltage amplitude. At the subsequent step we identified characteristic spatial and temporal covariance patterns by applying PCAs, in order to pick essential processes in each processing epoch and to relate them to the found condition differences. By focusing on these, we performed further analyses at some electrode locations and a source analysis in two selected processing epochs, aiming at a possible explanation of observed differences between conditions. Finally, based on theoretical assumptions and behavioral results, additional analyses were used, which deviated to some extent from a strong data driven hierarchical approach.

3.3 Results and discussion

3.3.1 Behavioral data

Delay duration

By manipulating the time between two imperative signals we intended to produce three delay ranges, which should be similar among eight target conditions. Table 3-2 provides an overview of the measured and averaged delay durations, as indicated by intervals between the end of the first backward movement and the time point of the reproduction tone in each experimental condition.

Table 3-2. Mean durations (in ms and standard deviations in brackets) between the end of the first backward movement and the second imperative Go-signal in the 24 experimental conditions.

Delay condition	*Target location*							
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
0	159(78)	176(78)	189(83)	215(86)	237(91)	262(99)	280(99)	288(109)
1	1132(83)	1152(96)	1156(105)	1183(100)	1206(103)	1219(112)	1235(119)	1235(124)
5	5081(95)	5102(98)	5104(108)	5135(107)	5150(113)	5160(130)	5174(136)	5170(134)

Apart from a slight increase in interval duration with an increase in distance within each delay condition, time manipulation was successful (Means (ms): delay “0” = 226, delay “1” = 1190, delay “5” = 5135).

3.3.1.1 Reaction times and errors

Figure 3-1 shows the distribution of over 24 experimental conditions averaged reaction times, constant and variable errors.

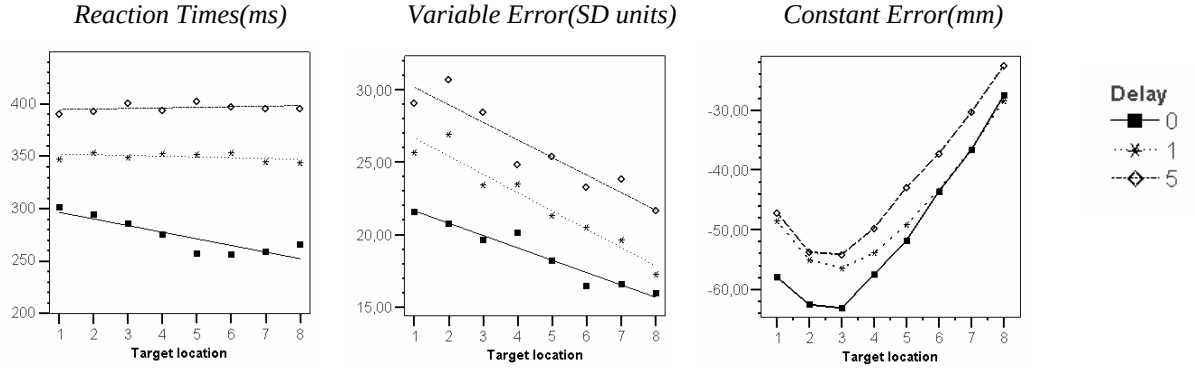

Figure 3-1: Mean reaction times, constant and variable errors as functions of distance and delay conditions. Note: lines are regression lines fitted to the data for each delay condition in case of reaction times and variable error. Negative values of constant error reflect the magnitude of overshooting.

The results of performed ANOVAs are summarized in Table 3-3.

Table 3-3: Main effects and interactions of the ANOVAs of reaction times, constant and variable errors, *p < .05; **p < .01. Note: all tests were adjusted according to the Greenhouse-Geisser method.

	Reaction Times			*Variable Error*			*Constant Error*		
Effect	df	F value	P value	df	F value	P value	df	F value	P value
Delay (D)	2,34	**45.2****	**<.001**	2,34	**35.2****	**<.001**	2,34	**5.4***	**.020**
Target location (T)	7,119	**5.5****	**.001**	7,119	**25.2****	**<.001**	7,119	**28.8****	**<.001**
D x T	14,238	**5.7****	**<.001**	14,238	1.2	.285	14,238	**2.4***	**.048**

All dependent variables were affected by the factors delay and distance. Reaction times increased with longer delays (M(“0”) = 276; M(“1”) = 350; M(“5”) = 401)), as expressed in a significant main effect for the factor “delay” and respective post hoc tests (all Ps <.001). There were also differences between target locations, in which an increase in covered distance tended to result in a decrease in reaction time (linear contrast for “distance”: F(1) = 12.3; P <.01). However, a significant “delay x target location” interaction suggested that these differences were only present in the shortest delay condition (see Fig. 3-1).

The variability of reproduction movements increased with longer retention intervals (sign. main effect “delay”; M(“0”) = 18,6; M(“1”) = 22,3; M(“5”) = 25,9), and all three factor levels differed significantly from each other as indicated by post hoc comparisons (all Ps <.05). Moreover, a main effect “target location” was significant and optimally approximated by a linear function (linear contrast: F(1) = 137,6; p <.001). This suggests that an increase in the covered distance was associated with a decrease in endpoint variability likewise in all delay conditions (due to a nonsignificant delay x target interaction, see Table 3-3).

The constant error was also affected by both factors, as indicated by corresponding significant main effects. However, the delay x distance interaction was significant too; suggesting delay dependent changes of distance differences, which obviously followed a non linear function with delay specific slopes (see Figure 3-1).

These results show that an increase in the retention interval resulted in higher reaction times, higher response variability and in changes of response tendencies. Moreover, all response parameters were affected by the movement distance with a decrease in variability and a reduction of reaction times in the shortest delay condition with increasing distance. Furthermore, there was a tendency of more overshooting up to the third target position, and from there up to the eighth location a decrease in overshooting size.

3.3.1.2 Kinematic data

Position, velocity and acceleration profiles for one trial and one subject are depicted in Figure 3-2.

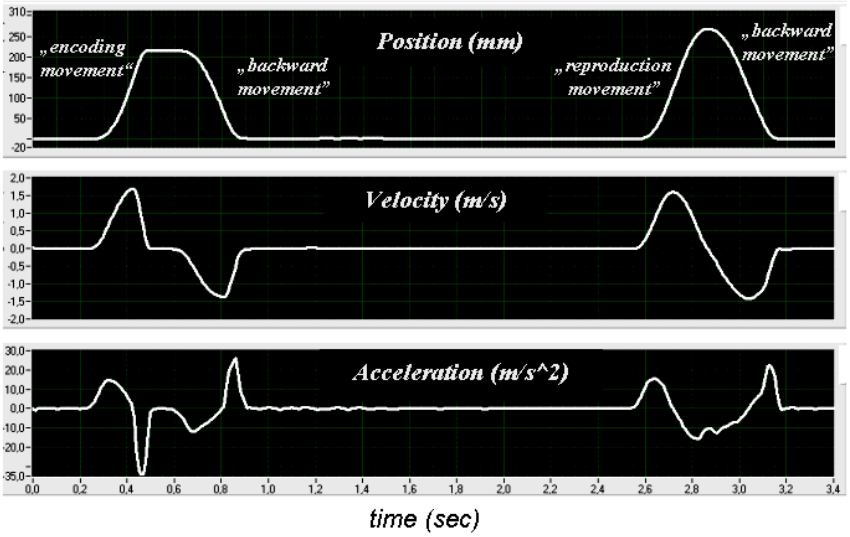

Figure 3-2: Kinematic trajectories of all movements performed within a single trial by one representative subject (target location 4 under delay “1” condition). Note: time scale is adjusted to the first imperative “Go” signal.

As expected, the movement kinematics were characterized by approximate linear hand movement trajectories and single-peaked velocity profiles, which were similar for forward and backward movements. However, for the “encoding movement” the velocity trajectory was usually not bell-shaped, due to mechanical braking, and the corresponding acceleration course had an atypical form.

Figure 3-3 shows the over all subjects averaged movement, velocity and acceleration profiles of the handle during reproduction movement. In all three delay conditions peak velocity increased significantly with increasing movement amplitude, as indicated by a significant main effect of factor “target location” (see Figure 3-4(B) for means and Table 3-4 for statistical results). Peak amplitudes were higher with shorter retention intervals (significant main effect “delay” and corresponding significant post hoc comparisons, all Ps<.05). Moreover, a significant “delay x target location” interaction suggested that distance differences were to some extent delay specific.

All delay conditions showed a similar scaling of peak velocities with target distance, as previously reported in the visuomotor area (e.g. Messier & Kalaska, 1999). In contrast, peak acceleration showed no significant amplitude changes in the delay “0” condition, as indicated by a nonsignificant main effect for factor “target location” in a delay specific ANOVA ($F(2.8) = 1.3$, $P = 0.28$). With longer retention intervals, the peak acceleration increased with distance and resulted in a significant main effect for factor “target location”. A significant “target location x delay” interaction indicated delay dependent changes for the eight target positions,

which is mainly caused by an increasing differentiation with a longer delay duration (see different slopes of regression lines in Figure 3-4(A) and Table 3-4 for statistical results). Moreover, peak acceleration decreased with longer retention intervals (all Ps<.01).

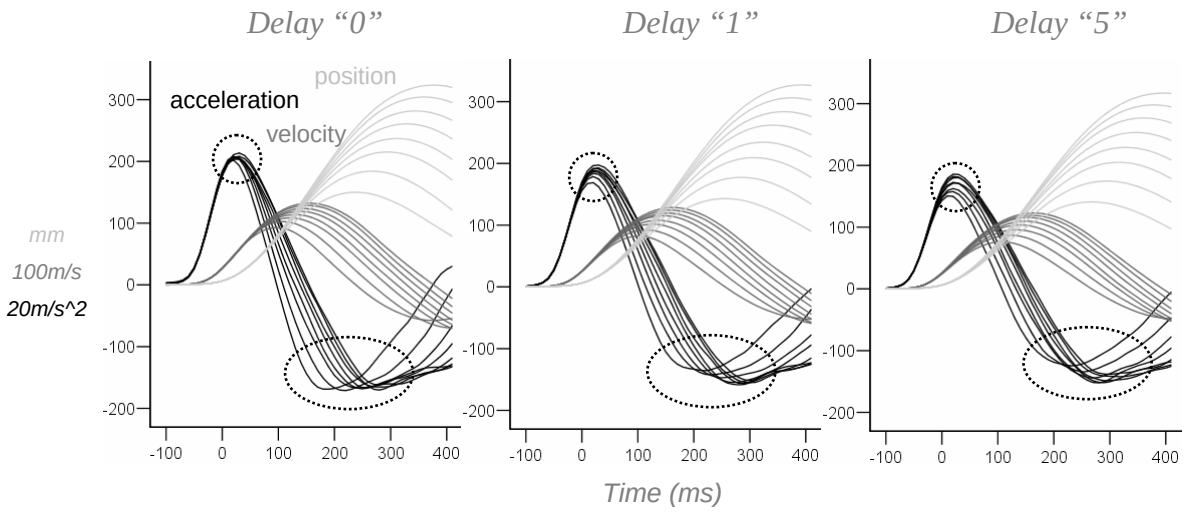

Figure 3-3. Kinematic parameters of the reproduction movements. Over all subjects averaged records are shown of position ( ), velocity ( ) and acceleration ( ) according to eight target locations under delay "0", "1" and "5" conditions. Note: all curves are synchronized to movement onset as defined in the method section. Peak acceleration and peak deceleration are marked with dotted lines in order to emphasize delay dependent changes of these parameters.

In the analysis of acceleration duration (or of the time to peak velocity) the "delay x target location" interaction was not significant (see Figure 3-4(C) and Table 3-4). This suggests a similar modulation of acceleration duration along the eight target positions in all three delay conditions. However, there were differences between target locations and delay conditions (corresponding main effects were significant) due to a prolongation of acceleration duration with longer distance and delay condition (all target positions differed from each other: Ps<.01; for delay levels only a trend was detectible by Bonferroni corrected post hoc comparisons: "0" vs. "5" – P = 0.08).

Since the area under the acceleration curves is directly related to the maximum velocity, these results reveal that in delay "0" condition , the main mechanism to achieve higher velocities with longer distance was a modulation of the acceleration duration. This is known as "pulse-width" control strategy (see discussion). Scaling of the peak acceleration amplitude in contrast is associated with "pulse-height" policy, which was observable in the longer retention conditions in addition to a similar duration modulation. Thus, the effect of the delay manipulation in the current experiment was related to a transition from quite poor pulse-width control to stronger contribution of pulse-height mechanisms when the retention interval increased.

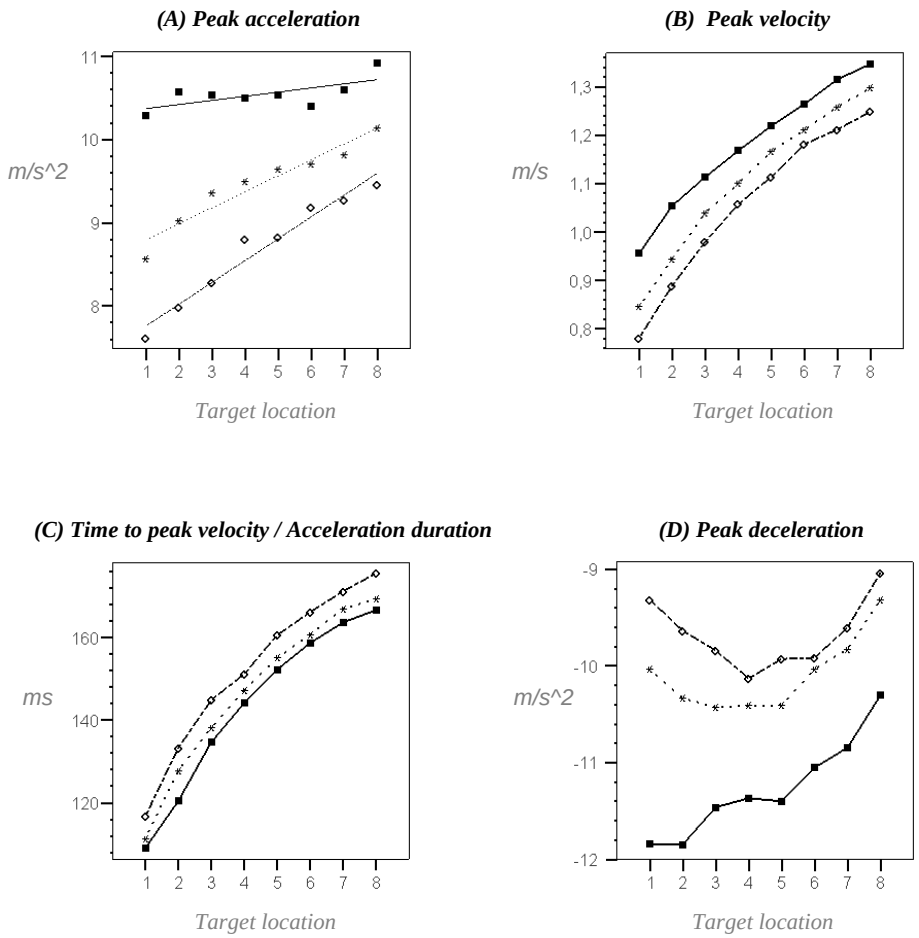

Figure 3-4: Averaged peak acceleration (A), peak velocity (B), acceleration duration (C) and peak deceleration (D) values. ■ = Delay "0", ✳ = Delay "1", ◇ = Delay "5". Note: lines in Figure (A) are regression lines.

Table 3-4: Results of performed ANOVAs. All tests were adjusted according to the Greenhouse-Geisser method.

Effect	*Peak acceleration*			*Peak velocity*			*Time to peak velocity*			*Peak deceleration*		
	df	F	P	df	F	P	df	F	P	df	F	P
Delay (D)	2,34	**21.5****	**<.001**	2,34	**22.2****	**<.001**	2,34	**4.1***	**.035**	2,34	**18.8****	**<.001**
Target location (T)	7,119	**25.0****	**<.001**	7,119	**277.0****	**<.001**	7,119	**167.4****	**<.001**	7,119	**7.0***	**.002**
D x T	14,238	**5.2****	**.001**	14,238	**5.2****	**<.001**	14,238	0.5	.825	14,238	**3.3****	**.006**

Furthermore, there were differences in peak deceleration with a similar distribution of amplitudes in the delay "1" and "5" conditions and higher values with a different trend across the eight target positions in the delay "0" condition (see Figure 3-4(D) and Table 3-4). While the direct reproduction was associated with an almost linear decrease in deceleration across the eight target locations, the trend was nonlinear in the two longer delay conditions: maximum deceleration increased with a maximum at a middle position (4 or 5), then decreased.

In order to investigate the functional role of peak acceleration and peak velocity, we correlated endpoint amplitude and duration of the first and second movements with the peak acceleration and peak velocity of the reproduction movement on a trial-by-trial basis (N(“0”) = 4003, N(“1”) = 3884, N(“5”) = 3902). The results of these analyses are shown in Figure 3-5.

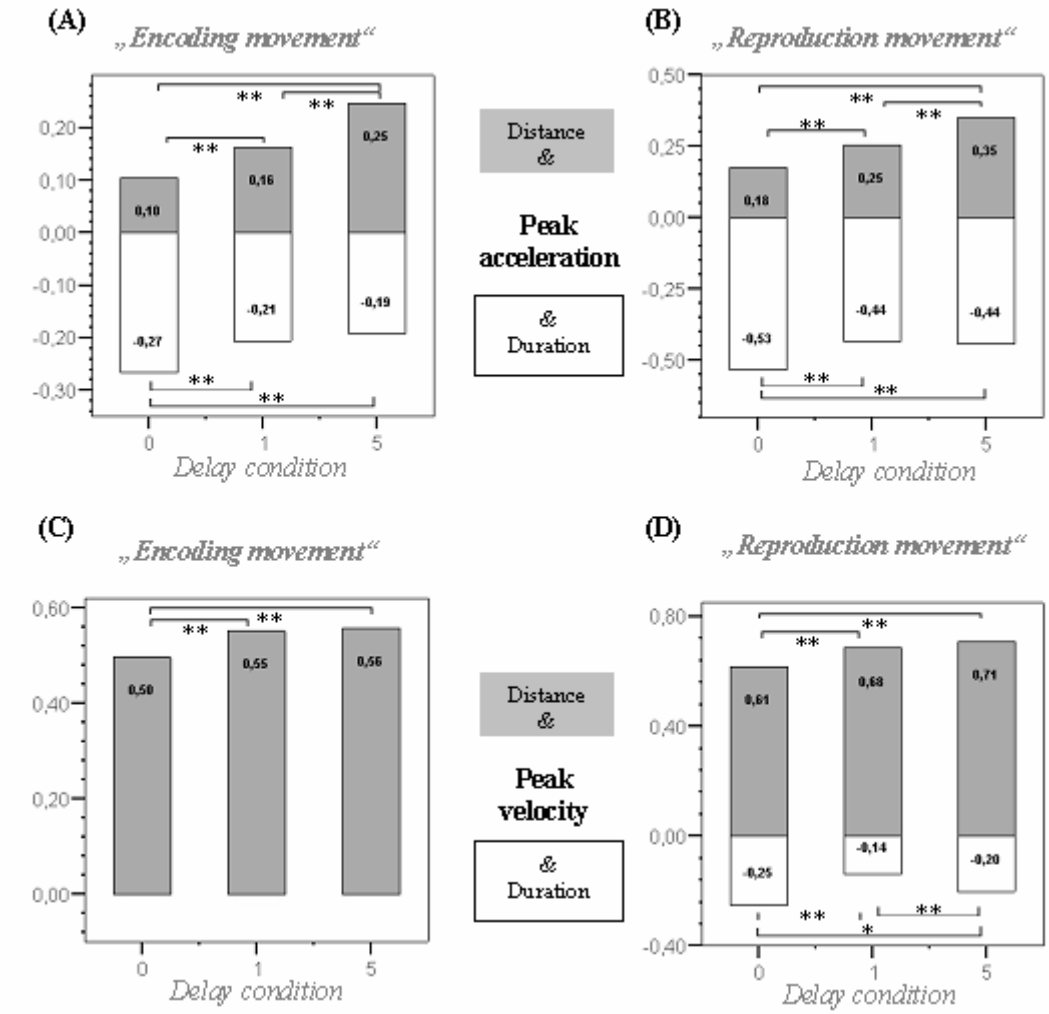

Figure 3-5: Significant correlation coefficients indicating a relation of peak acceleration of the reproduction movement to amplitude (gray bars) and duration (black bars) of the first movement (A), to the amplitude and duration of the reproduction movement (B). (C) and (D) represent significant correlations of peak velocity with the distance and duration of both movements. Differences between delay conditions were analyzed by a method described in the method section and depicted as * if $p < .05$ and ** if $p < .01$.

The distance of the first movement predicted the peak acceleration better the longer the delay was (see Figure 3-5(A)). A similar relationship was obtained between peak acceleration and the end position of the reproduction (Figure 3-5(B)). In contrast, the shortest delay condition showed a stronger relation to the duration of both movements than both other retention conditions (Figure 3-5(B) and (C)). Peak velocity showed a similar trend with delay “0” condition weaker related to the endpoints of both movements than the longer intervals. While there were no significant correlations between the duration of the first movement and the peak

velocity, the duration of the second movement was best predicted by the shortest delay condition again, followed by delay “5” and delay “1”. These results suggest that initial kinematics, like peak velocity and peak acceleration, are differently related to movement control parameters as indicated by high correlations between peak velocity and distance and between peak acceleration and the movement duration. Moreover, since end point distance reflects a static parameter, while the movement duration is more related to movement dynamics, the result suggests that the prolongation of the retention interval caused significant changes of movement control from dynamic to more static aspects.

In Figure 3-6 (A) averaged acceleration profiles of the encoding and the reproduction movements are superimposed, Figure 3-6 (B) shows the corresponding averaged peak accelerations.

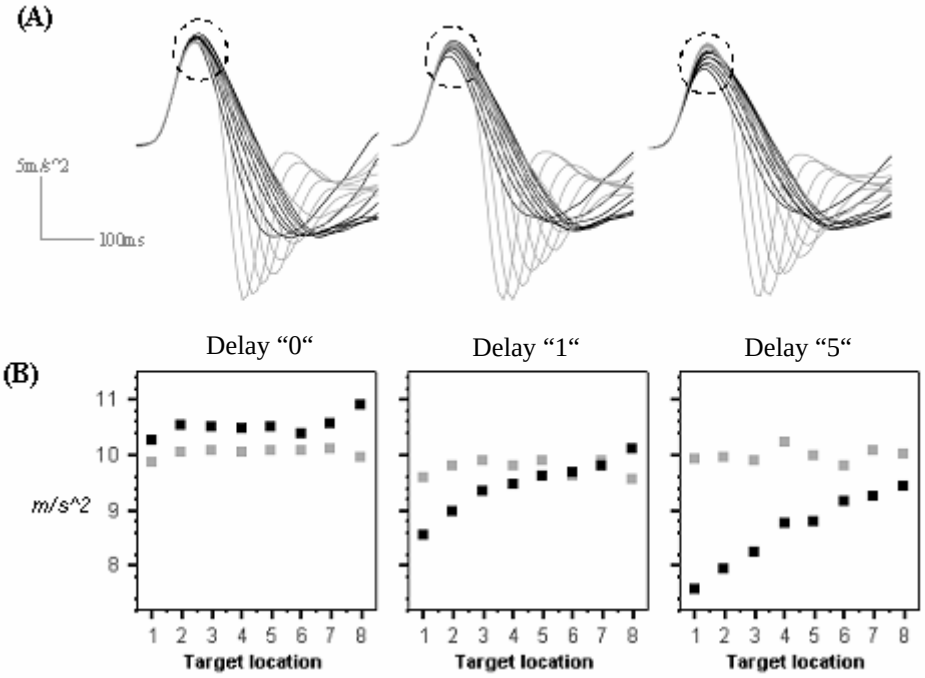

Figure 3-6: Averaged acceleration profiles of first (gray) and second (black) movements (A) with corresponding means of peak acceleration (B) under three delay conditions.

ANOVAs with “delay” and “distance” factors revealed no significant differences for variable “peak acceleration” of the first movement (Main effect “delay”: $F(2) = 1.3$, $P = 0.3$; “delay x distance” interaction: $F(6.1) = 1.1$, $P = 0.4$). ANOVAs for each delay condition with factors “distance” (8) and “type of movement” (2: encoding and reproduction) showed that in delay “0” both movements did not differ statistically. Peak acceleration gradually decreased in longer delay conditions at near target locations (Delay “1”: main effect “distance” - $F(4.4) = 8.7$, $P<0.001$, interaction “distance x type of movement” – $F(4.1) = 10.8$, $P<0.001$; delay “5”: main effect “distance”- $F(5.1) = 16.9$, $P<0.001$, main effect “type of movement” – $F(1) =$

12.4, P = 0.003, interaction – F(3.4) = 17.4, P<0.001; see Figure 3-6(B) for means). These results suggest that the initial pulse during encoding movement was too high for near target locations and had to be reduced during reproduction (see discussion). However, in the shortest delay condition the subjects did not do this. Instead, they obviously followed the “first” pulse and shortened only acceleration and / or movement duration in order to reach different distances.

Discussion

By analyzing the reaction times and the two error types, we detected delay and distance dependent differences. A longer retention interval caused, as expected, a successive deterioration of performance, expressed by an increase in reaction times and response variability. However, these results do not necessarily speak for “qualitative” changes in processing characteristics and may merely result from an increase in noise.

The standard deviations as well as the reaction times in the shortest delay condition decreased with increasing distances, suggesting performance improvement with longer movements. This finding is at variance with established findings of motor control (e.g. Harris & Wolpert, 1998).

According to a computational view of sensorimotor interactions during movement execution, the CNS integrates sensory input and motor output signals in an adaptive way (for review see e.g. Van Beers et al. 2002, Wolpert & Ghahramani, 2000). This combination is used to compensate for sensorimotor delays and to reduce the uncertainty resulting from sensory and motor related noise. Based on motor command information (e.g. “efference copy”), the system is assumed to predict sensory consequences and to update them with the actual sensory feedback as soon as this is available. The subjects in the present study were blindfolded and were instructed to move their hand after the first imperative signal to an undefined position until they reached a stop. Since the stop position was unpredictable and subjects were asked to perform rapid uncorrected movements, it can be assumed that subjects initially aimed at a “far” position as the default. This prediction is confirmed by the acceleration profiles of the first movement, as peak amplitude did not differ and the profile approximated a typical biphasic form with longer distances. Moreover, peak acceleration successively decreased during reproduction under longer delay conditions. If the subjects really aimed with the first movement to a far position, the motor command should deviate less from the sensory feedback signal, if the distance gets longer. Consequently, a process of

updating sensory and motor information should become easier and one may expect that the memory trace should be more stable with longer distances.
Moreover, the constant error followed a nonlinear function in all delay conditions, with a trend toward more "overshooting" from the first until the third target position and more "undershooting" in the longer distance conditions. A possible explanation could be provided by the "kalman filter model" (Wolpert et al. 1995), which predicts stronger overshooting with increasing dominance of motor outflow information and a contrast trend with stronger involvement of sensory feedback within the postulated control mechanisms, as a consequence of a different movement time dependent weighing of both information sources.
Delay differences, related to the constant error, were expressed in a decrease in overshooting, if considering only the shortest and the longest condition. This result resembles a well-known "empty interval effect" obtained in several early studies, which is associated with a shift of biases in the direction of underestimation over a delay interval (e.g. Laabs & Simons, 1981).

The analysis of early kinematic parameters revealed delay dependent differences in the control of the reproduction movement. We observed a similar gradual change of peak velocity with longer movements in all delay conditions. However, the strategy to achieve these velocities seems to depend on the retention interval. With immediate reproduction the subjects showed no significant changes of peak acceleration, but longer acceleration durations. In longer retention intervals changes of peak velocity were associated with corresponding changes of peak acceleration, which supplemented the modulation of movement duration changes.
Acceleration, as well as position and velocity changes are assumed to result from two central commands, a "pulse" signal[7], which provides the driving force for setting the limb in motion, and a "step" component, which controls the terminal steady state force (e.g. Ghez & Vicario, 1978). This "pulse-step model" was initially formulated for eye movements (Robinson 1973) and was later also used to describe arm movements (Ghez & Vicario, 1978, Ghez, 1979, Barto, Fagg, Sitkoff, & Houk, 1999, Gottlieb et al. 1989, Karniel & Inbar, 1999, Feldman & Levin, 1995, Suzuki & Yamazaki, 2005). Both command components – pulse and step – are assumed to be visible in EMG recordings[8], which are closely related to acceleration and deceleration profiles (Gordon & Ghez, 1984, Ghez & Gordon, 1987; Gordon & Ghez, 1987a ; Brown & Cooke, 1990, Cooke & Brown, 1994, Gottlieb et al., 1989). For example, Ghez and

[7] E.g. as neural input to the alpha motor neuron pools, see Gottlieb, Corcos, & Argawal, 1989.
[8] which are considered as low pass filtered versions of controlling signals to the motoneuron pools, see e.g. Gottlieb et al. 1989.

Gordon (1987) reported close temporal associations between peak acceleration and the peak of the first agonist EMG, and peak deceleration and the antagonist EMG activity for monotonic flexion force impulses at the elbow.

Research has also shown that the peak amplitude of acceleration and the first agonist EMG burst (labeled as AG1) co-vary with peak velocity and movement extent (Gordon & Ghez, 1987a, Gottlieb et al., 1989, Messier & Kalaska, 1999, Sainburg & Schaefer, 2004, Bagesteiro, Sarlegna, & Sainburg, 2006). This mechanism is labeled as "pulse height" control policy. In contrast, if a different distance and / or peak velocity is achieved by modulation of acceleration duration (or AG1 duration) (Brown & Cooke, 1984, Cooke & Brown, 1994, Gottlieb et al., 1989, Sainburg & Schaefer, 2004, Bagesteiro et al., 2006), one speaks of a "pulse-width" control strategy.

There is evidence that the two control strategies represent independent aspects of motor control. It was repeatedly reported that the duration of AG1 is strongly related to the movement time or to the rise time of force (e.g. Brown & Cooke, 1990, Benecke, Meinck, & Conrad, 1985, Schmidt, Sherwood, & Walter, 1988, Ghez & Gordon, 1987, Wallace, 1981, Wallace & Wright, 1982) whereas intensity of AG1 (or second derivate of force) co-varies with peak velocity and movement distance (Wallace, 1981, Brown & Cooke, 1981, Hallet and Marsden, 1979, Ghez & Vicario 1978). Accordingly, Gordon and Ghez (1987b) suggested that the pulse-width modulation is a compensatory mechanism, which adjusts the movement time to inaccuracy in pulse-height control of force pulses. This proposal was supported by further studies of visual guided movements, indicating that the amplitude of initial kinematics is reciprocally related to movement duration (Gordon, Ghilardi, Cooper, & Ghez, 1994, Messier & Kalaska, 1999).

"Pulse-height" modulation seems to be relevant if tasks require control over speed or movement time, whereas "pulse-width" modulation controls movements of different distances without additional constrains on speed or accuracy[9] (Gottlieb et al., 1989).

More recently, Sainburg and Schaeffer (2004) reported a "pulse-width" control strategy, when subjects produced hand movements to visual targets with their left hand. In contrast, right hand movements were associated with a "pulse-height" policy. Since the "pulse-width" mechanism depends more on sensory feedback than the "pulse-height" mechanism, the

[9] According to Gottlieb et al. (1989) pulse-height modulation can be expected in experiments with the following characteristics: (a) movements of fixed distance (and loads) in a explicitly specified duration (b) movements of constant duration with different distances / loads (c) explicitly control of movement speed (d) Manipulation of accuracy constrains. Pulse width control strategy should be preferred, if subjects do not adopt explicit control over the speed, like in situations, where movements to different distances are performed without explicit speed or accuracy manipulation.

authors concluded, that “pulse-height” control is related to open-loop processes, while “pulse-width” control reflects feedback mediated closed-loop processes. By manipulating the congruency between actual and visually presented information about the start position of hand movements to visual targets, Bagesteiro et al. (2006) demonstrated that subjects preferred “pulse-width” control if the initial hand position was indicated by propriception, and a “pulse-height” strategy if visual feedback was available. Thus, “pulse-height” modulation was related to feed-forward planning based on visual information, while “pulse-width” as reflected by a variation of acceleration duration, was assumed to reflect sensory based correction processes. Although evidence supports the idea that the “pulse-high” control is related to preplanning and the “pulse-width” strategy to sensory feedback mechanisms, this conclusion should be considered with caution. Gordon and Ghez (1987b) noted that compensatory adjustments must primarily depend on internal feedback loops, because they occur too fast for being dependent on peripheral feedback mechanisms. Moreover, the authors pointed out “if pulse width is preprogrammed by the nervous system, our method would underestimate the contribution of motor programs to the control of this behavior” (Gordon & Ghez, 1987a). Thus, “pulse-height” and “pulse-width” modulation are not necessarily compatible with the distinction between open-loop and closed-loop processes, because sensory feedback mechanisms may be essential in the late phase of a movement. We observed in our study that a longer delay was associated with a tending towards more “pulse-height” control influences. Simultaneously, movements got slower and therefore could also be more affected by sensory feedback. In addition, it cannot be excluded that acceleration and movement duration, can also be specified in a feed-forward manner. In this case “pulse-width” modulation would simply reflect another control parameter that may or not be affected by afferent feedback. Based on previous research of functional brain asymmetry in motor control, Sainburg and Schaeffer (2004) suggested that the “pulse-width” strategy could be responsible for control of final position or posture, and “pulse-height” strategy for trajectory planning. However, our results are not compatible with the idea that modulation of acceleration duration – “pulse-width – is related to control of static variables, as posture or position, and the “pulse-height” strategy reflects dynamic control (e.g. trajectory). Instead, our correlation analyses suggest rather an inverse relationship between both mechanisms (“pulse-high” and “pulse-width”) and the control of static and dynamic parameters. The correlation between the distances of both movements and the amplitude of peak acceleration of the reproduction movement increased with longer delays, while simultaneously, the correlation between movement duration and peak acceleration decreased. This suggests that an increase in “pulse-height” control may

rather be related to an increase of static control parameters (e.g. end position, end posture, movement distance), which seem to be especially relevant in longer delay conditions. In contrast, a rather “poor” “pulse-width” strategy, obtained in the short delay (“0”) condition was associated with a high relation to a dynamic variable (movement duration), and consequently may rather reflect dynamic control aspects.

Furthermore, in a previous experiment we examined how static and dynamic information depend on delay length by asking subjects to reproduce a target position or a moved distance from a varying start position. We observed that independent of delay length, peak acceleration co-varies only little with the target amplitude in the distance condition (“pulse-width”) and much stronger if positions were to be reproduced (“pulse-height”). Moreover, peak deceleration decreased with movement length, when distance was reproduced and rather increased, when position reproduction was required. We concluded that the subjects followed the “unnatural” spatiotemporal characteristic of the encoding movement in the distance condition, and “corrected” this, when movements to terminal locations were performed. The distance specific changes of peak deceleration in the short delay condition of the current study resembles the results of the distance condition of the prior experiment and the peak deceleration scaling obtained in longer delay conditions seems to be similar to the position reproduction condition. In addition, we found that peak acceleration was more closely related to movement duration in the distance condition than in the position condition, while the correlation of peak acceleration with movement distance showed an opposite relationship. The analysis of peak velocity revealed similar results. These observations seem to confirm the conclusion that the extension of delay in the present study was associated with a decreasing influence of dynamic and an increasing influence of static control variables.

In conclusion, we suggest that a modulation of acceleration duration is related to the control of dynamic variables (like movement duration or dynamic trajectory control), whereas a distance-specific scaling of peak acceleration seems to indicate a dominance of static control (like end posture or end position). This assumption seems to be confirmed also by studies, which reported strong relations between movement time and AG1 duration, and between intensity of AG1 and movement distance. It is also compatible with compensatory mechanisms, suggested by Gordon and Ghez (1987b), which were attributed to a “pulse-width” modulation. By comparing encoding with reproduction movements, we observed that peak acceleration values of both movements were not significantly distinct in the shortest delay condition. The modulation of peak acceleration in longer delay conditions was due to a successive decrease in the amplitude with shorter distances. This seems to indicate that the

first pulse was too high for near target positions and had to be adjusted during reproduction. Adjustments, which occur in the shortest delay condition, can be interpreted as “compensatory” according to Gordon and Ghez. Although similar mechanisms may be important in the longer delay conditions, additional modulation of peak acceleration indicates a change of “error correction” in the direction of offline modification of the initial impulse, which better predicts the aimed endpoint.

However, the proposed relationships between dynamic control and pulse-width and static control and pulse-height seem to be far from simple. While the magnitude of acceleration was related to duration, peak velocity showed a stronger relation to the moved distance, suggesting a different contribution of both measures to the dynamic and static control mechanism. Moreover, the amplitude of peak deceleration also varied as function of delay length, suggesting different deceleration strategies across delay conditions.

It remains an open question to what extent the findings are task and / or modality specific. Nevertheless, our results indicate that the time between encoding and reproduction may change control parameters. These changes were expressed in a transition from a dynamic to more static control strategy in the given experiment.

3.3.2 Event Related Activity

Figure 3-7 shows the averaged waveforms contingent to the movements to the sixth target position and measured from one second before the first imperative stimulus until 500ms after the end of the second backward movement at three midline electrode locations (FZ, CZ, PZ).

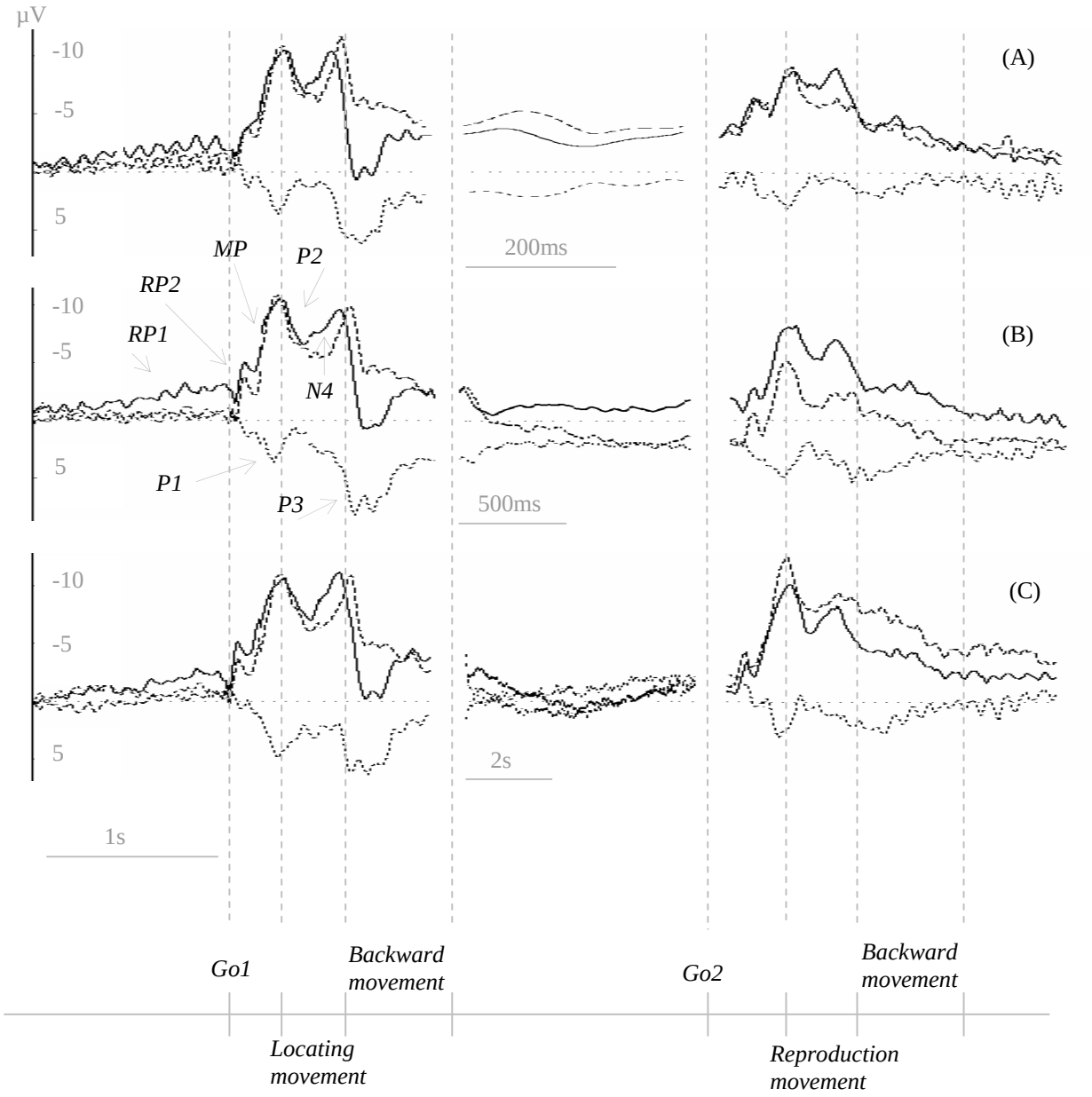

Figure 3-7. Evoked potentials of movements to the sixth target location at FZ (——), CZ (- - -) and PZ (.....) under delay "0" (A), delay "1" (B) and delay "5" (C) condition. At the bottom of the Figure, there are marker positions, indicating time points of both imperative signals (Go1 and Go2) and the time ranges of all movements. Note: To reduce variability, all potentials were adjusted to each trigger and the interval between –2000 and –1000 ms before the first imperative tone served as baseline; ERPs of the delay epoch were filtered with 5 Hz low pass filter and their timescales were adjusted to cover an interval of equal size.

The visual inspection of the data indicates a sequence of components that were also previously observed before and during simple self-initiated ballistic movements (for review

see Brunia, 1987, Brunia & Van Boxtel, 2000). Although the present study differs from the traditional “Bereitschaftspotential” paradigm, we nevertheless adopted known component labels for a first classification.

The first premovement negative shift is most likely related to the early part of the “Bereitschaftspotential” (or “readiness potential”), which typically shows a symmetrical distribution over central and parietal areas and which is associated with motor presetting or preparation processes (RP1). After the first imperative stimulus a second potential arises, the lateralized portion of RP (RP2), this is assumed to represent response selection mechanisms. The next component preceding the movement onset is the “premotion positivity” (P1), whose role is still under debate. The last premovement negative deflection is the “motor potential” (MP) traditionally assumed to represent the command to move. The positive wave following the MP (P2) as well as the next negative (N4) and positive waves (P3) have been related to sensory feedback mechanisms.

The potentials of locating and reproduction movements are highly similar. However, as shown in Figure 3-7, some differences exist, the negative wave at FZ, as well as the P3 component at PZ are less pronounced during the reproduction movement. ERPs of all target and delay conditions at selected electrodes can be found in the Appendix (3-B, 3-C, 3-D, 3-E, 3-F).

3.3.2.1 “Sensitive time windows”

As the first step of the analysis, we performed several ANOVAs with the within-subject factors “distance” (8 levels), “delay” (3 levels) and “electrode” (61 levels) and mean voltage amplitude of each time window as dependent variable. Table 3-5 collects F and P values for the critical interactions: “electrode x distance” (ELxDS) and “electrode x delay” (ElxDL). None of the other interactions reached the significance threshold indicating that both factors (delay and distance) affected the mean voltage amplitude independently from each other (see Appendix 3-G).

Time window specific ANOVAs delineated several time segments, in which the mean amplitude of ERPs was influenced by different distances or different delays (or both). Since the large number of 61 electrodes can influence alpha-error, we also ran the same analyses with only 17 electrodes (standard position). Apart from two time windows, in which two additional interactions became significant (RM phase, 200-250ms, ElxDL; MP phase, 200-250ms, DSxDL), all results for 17 and 61 electrodes were equivalent. In order to enable a

better spatial resolution of significant effects, we performed the following "electrode specific" analyses by including all 61 electrode locations.

Table 3-5: Results of time window specific ANOVAs; * p(F) <.05; **p(F) <.01;LM = locating phase, RM = reproduction movement, S = processing after the stop, MP = motor programming, D = delay phase. Note: all tests were adjusted according to the Greenhouse-Geisser method.

		Measurement Interval											
Phase	*Interaction*	*0-50ms*		*50-100ms*		*100-150ms*		*150-200ms*		*200-250ms*		*250-300ms*	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
LM	*ElxDS*	0.9	.527	1.0	.479	1.5	.131	**5.1****	**.000**	**7.2****	**.000**	**13.1****	**.000**
	ElxDL	1.3	.278	1.6	.160	0.9	.499	1.1	.400	2.1	.055	1.9	.079
RM	*ElxDS*	1.2	.318	1.0	.444	**2.4***	**.010**	**2.8****	**.004**	**3.5****	**.000**	**5.5****	**.000**
	ElxDL	**3.0***	**.014**	**2.4***	**.037**	**2.8***	**.017**	2.1	.089	2.2	.069	**2.9***	**.023**
S	*ElxDS*	**5.1****	**.000**	**9.3****	**.000**	**3.6****	**.001**	**3.2****	**.004**	**4.9****	**.000**	**4.5****	**.001**
	ElxDL	1.4	.228	1.3	.258	1.7	.137	1.0	.404	1.0	.451	0.9	.480

		100-150ms		*150-200ms*		*200-250ms*		*250-300ms*		*300-350ms*		*350-400ms*	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
MP	*ElxDS*	0.8	.594	1.0	.464	0.7	.730	1.0	.472	1.0	.481	1.5	.159
	ElxDL	**3.8****	**.004**	**4.5****	**.001**	**4.6****	**.001**	**3.6****	**.007**	**9.2****	**.000**	**17.3****	**.000**

		Time range I		*Time range II*		*Time range III*	
		F	*P*	*F*	*P*	*F*	*P*
D	*ElxDS*	**2.2****	**.014**	**2.2****	**.014**	**2.2***	**.020**
	ElxDL	**5.2****	**.000**	**5.7****	**.000**	**4.0****	**.000**

3.3.2.2 Locating movement (LM)

We reduced the dimensionality of the dataset by using spatial PCAs in this time range. The "eigenvalue equals one rule" indicated four components, while the scree test indicated only three. However, only the first two components explaining 81 % of total variance were stable over the different matrices and rotations. Their loadings and scores are shown in Figure 3-8 (left), together with the topography of the measured activity at the hypothetical activity maximum, as well as the ERPs at selected electrodes (Figure 3-8, right).

The first component (F1) accounted for 44% of the variance showed a centroparietal-frontopolar topography and an early activity maximum (~ 80ms), which was followed by a second peak in conditions with longer movements. Component F2 explained 37% of the variance and has a frontocentral maximum. Its time course indicates an initially decreasing and then increasing activity. Both components were affected by the distance manipulation

differently. Obvious effects occurred earlier in the first component (starting at about 150 ms) than in the second (starting at about 200ms).

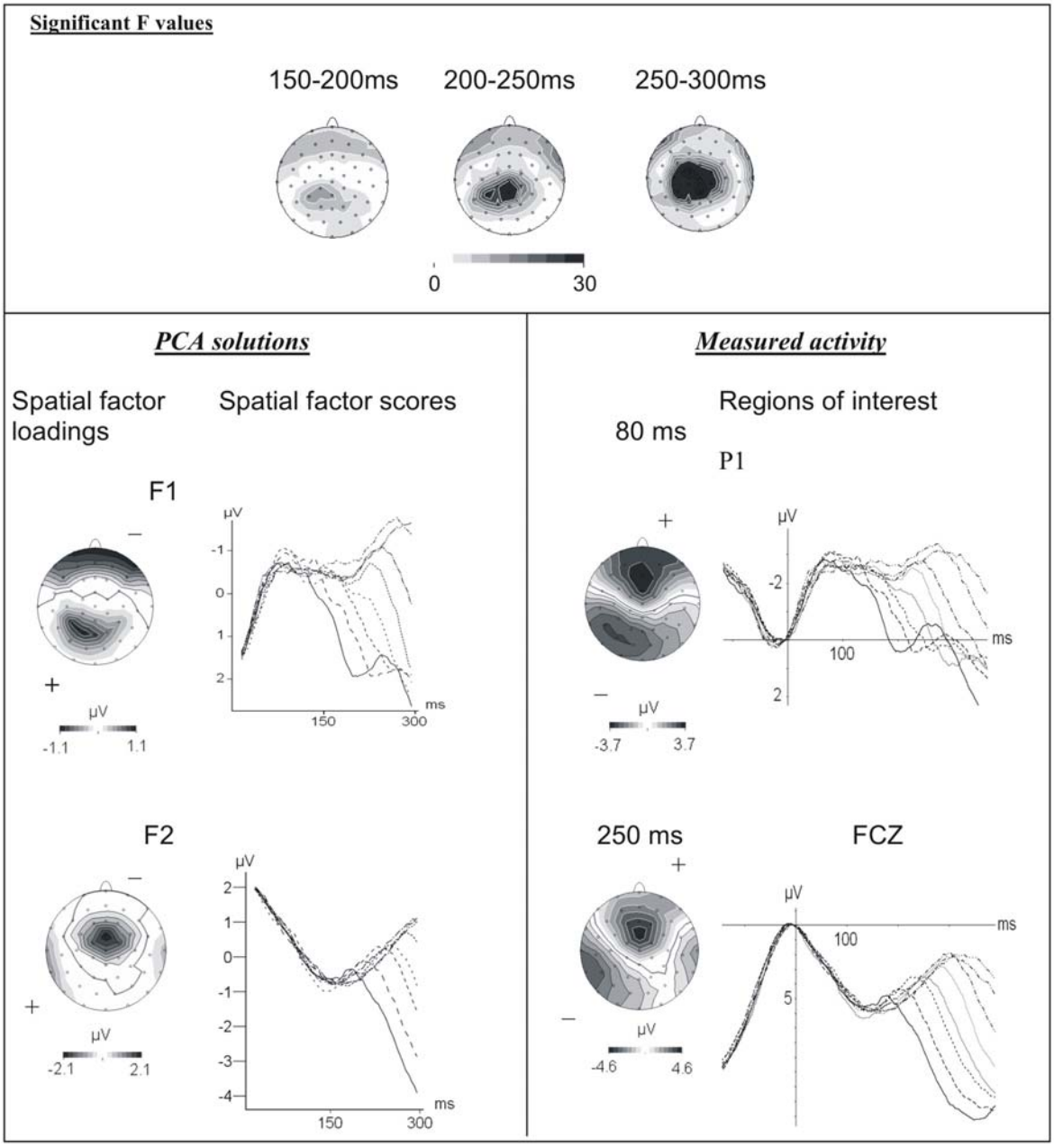

Figure 3-8. *Top*: linear interpolated F values of main effect "distance" at electrodes, where Greenhouse-Geisser corrected P scores were <.05.; *left*: results of PCA decomposition; *right*: topography of ERPs (averaged over all distances and delays) at 80 and at 250ms after the movement onset and ERPs of 8 distances (averaged over all delay conditions) at electrodes P1 and FCZ. All time scales are adjusted to the onset of movements. The type of line reflects 8 target locations: 1 2 3 4 5 6 7 8

In the locating movement phase (LM) we found significant electrode x distance interactions between 150 and 300ms indicating that the distances affected the mean amplitude differently

at different scalp sites (see Table 3-5). The results of electrode-specific ANOVAs are depicted as linearly interpolated F values of the main effect “distance” in the upper part of Figure 3-8. The main differences between the movements of different length were present at centroparietal electrodes. Moreover, the topography of the F scores indicated a leftward shift, which seemed to drift over the time from left centroparietal to frontocentral regions.
Following the PCA results we restricted the “regions of interest” to a left posterior (P1) and a middle frontocentral (FCZ) electrodes.
Post hoc comparisons at P1 indicated that the mean negative amplitude increased monotonically with longer distance (e.g. follow comparisons reached significance in the 200-250ms time window (all Ps<.05): 1vs5,6,7,8; 2vs4,5,6,7,8; 3vs5,6,7,8; 4vs7).
Similar effects were evident at frontocentral locations, especially in the last time-window. We analyzed this activity further by a peak to peak analysis applied to the ERPs measured at FCZ. For this purpose we searched for the most positive and the most negative peaks at FCZ within the time range between 100 and 400ms in the individual averaged ERPs[10]. The amplitude-difference of these two peaks and the latency of the negative peak were analyzed with an ANOVA with “distance” (8) and “delay” (3) as within-subject factors. The analysis of the amplitude revealed a significant main effect for the factor “distance” (F = 15.2, P< .001) and a highly significant linear contrast (F=24.7; P<.001), suggesting a roughly linear increase of the negative peak relative to the maximum of the prior positive deflection with increasing movement length (see Figure 3-9(A) for mean values of the 8 target conditions). None of the other effects reached the significance threshold (all Ps > .05). Only a main effect “distance” was also evident in the latency measure of the negative peak (F= 107.0; P<.001). As shown in Figure 3-9(B), the latency increased linearly with an increase in the movement distance, expressed also in a significant linear contrast (F=251.5; P<.001).

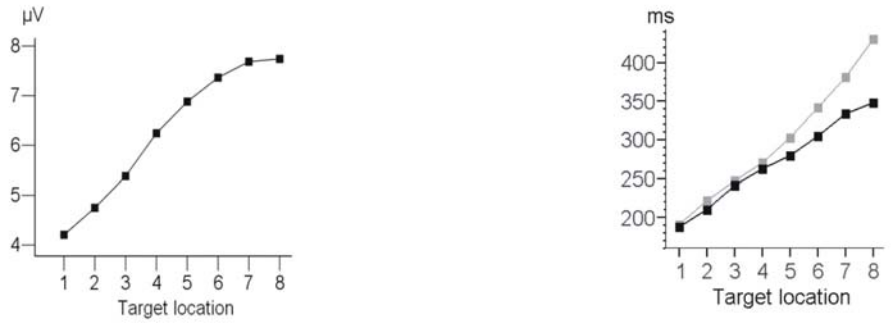

Figure 3-9. (A) means of the amplitude difference between the positive and the negative maxima at FCZ (B) latency of the negative peak at FCZ (—■—) and averaged movement duration until the stop (—■—).

[10] Time windows were adjusted based on grand average and were +/-60ms around the peak of respective distance.

Figure 3-9 (B) also contains the averaged movement duration until the stop was reached. This shows that the latency of the negative peak corresponds quite precisely with the averaged movement duration for the first four target positions, whereas for longer distances the peak latency precedes the end of the movement with a gradual increase in this discrepancy.

Discussion

By using PCAs we could identify two components, whose spatial factor loadings seem to correspond rather well with the topographical distributions of mean amplitude differences between the eight distance conditions, detected by the performed ANOVAs.
The activity at posterior recording sites, whose variance was bound by the F1 component can be described as an initially negative going wave with a distance specific duration of this negativity. An increase in movement distance was expressed in an increase in latency, at which the ERPs became positive going. Thus, the distance differences seem to be mainly related to the duration of a process taking place during movement execution.
The topography of these distance effects and the initial ERP dynamic at posterior electrodes is similar to the P1 wave[11], a positive deflection preceding movement onset, which has been attributed to the activation of corticospinal pathways (Gilden, Vaughan, & Costa, 1966), to the command to move (Deecke & Kornhuber, 1977), or to the inhibition of mirror-movements (Shibasaki & Kato, 1975). By following this, one may speculate that some inhibition or deactivation processes expressed in P1 may also take place during movement execution.
The highest loadings of the second PCA solution were localized over central and frontocentral regions with a biphasic activation course. The distance effects were maximal in the late time-window at these locations, and were expressed in a latency and an amplitude modulation of a negative going wave starting from about 120 ms after movement onset. An increase in movement distance was associated with a gradual increase in its peak latency and the peak amplitude. We labeled this component as N4 according to Brunia (1987). Similar negativities following the first positive deflection (P2) were reported over parietal, postcentral and precentral regions and were related to sensory feedback functions (Brunia, 1987). However, the performed PCA analysis indicated that primarily precentral electrode locations were associated with this deflection. The visual data inspection revealed that maximal amplitudes

[11] With reference to a “rest” baseline, e.g. to –2000 –1000ms in respect to the imperative Go-signal (see Figure 3-7) the activity over parietal electrodes can be described as initial positivity starting with the acoustic Go-signal and lasting shortly before the movement onset with subsequent decline of this activity.

of N4 were present at CZ, FC1 and CP1 suggesting the role of regions locating close to the primary motor cortex of the left hemisphere as sources of activity. If so, then some executive mechanisms would appear to be likely to be expressed in the N4 rather than sensory feedback functions.

In summary, the findings show different dynamics over postcentral and precentral regions and distance specific characteristic of activation. Moreover, since the target position is unknown before the stop, it has to be assumed that all movements were similarly pre-planned and controlled, probably by aiming at a far position (see discussion of the behavioral data). Thus, the "growing" negativity at central and frontocentral sites would represent a process, which takes place during the second half of the movement. It seems to be disrupted in the present processing phase, but in a distance dependent manner (see Figure 3-9).

3.3.2.3 Processing after the stop (S)

Significant differences between movements of different length were present in all analyzed time windows during the first 300 ms after the stop (see Table 3-4). The topographical maps of electrode specific F scores for factor "distance" (see Figure 3-10, top) indicated the largest values in the first two time windows localized around central sites. In contrast, the later differences had a broad frontooccipital topography.

The spatial PCAs yielded two stable components explaining 88% of the variance in this processing epoch (Footnote: five components had eigenvalues greater one, scree test suggested two up to four factors). Figure 3-10 illustrates their loadings and scores (bottom left) in comparison to the measured activity at the chosen time points and electrodes (bottom right).

The PCA component F1 (66%) showed a frontooccipital topography with obvious differences between different target conditions during the second half of the analyzed time window. The significant differences of the average amplitude between 150-300ms after the stop seem to be associated with this PCA component due to similar topographies of spatial factor loadings and the F value distributions.

The mean amplitudes at FZ in the time window 250-300ms read 1.65, 2.39, 3.51, 4.71, 5.16, 5.44, 5.01, 5.11 for target locations 1,2,3,4,5,6,7,8. Post hoc comparisons revealed significant differences (Ps.<.05) 1vs. 3,4,5,6; 2 vs. 4,5,6; 3 vs. 1, suggesting a trend towards less positive amplitude for short distances.

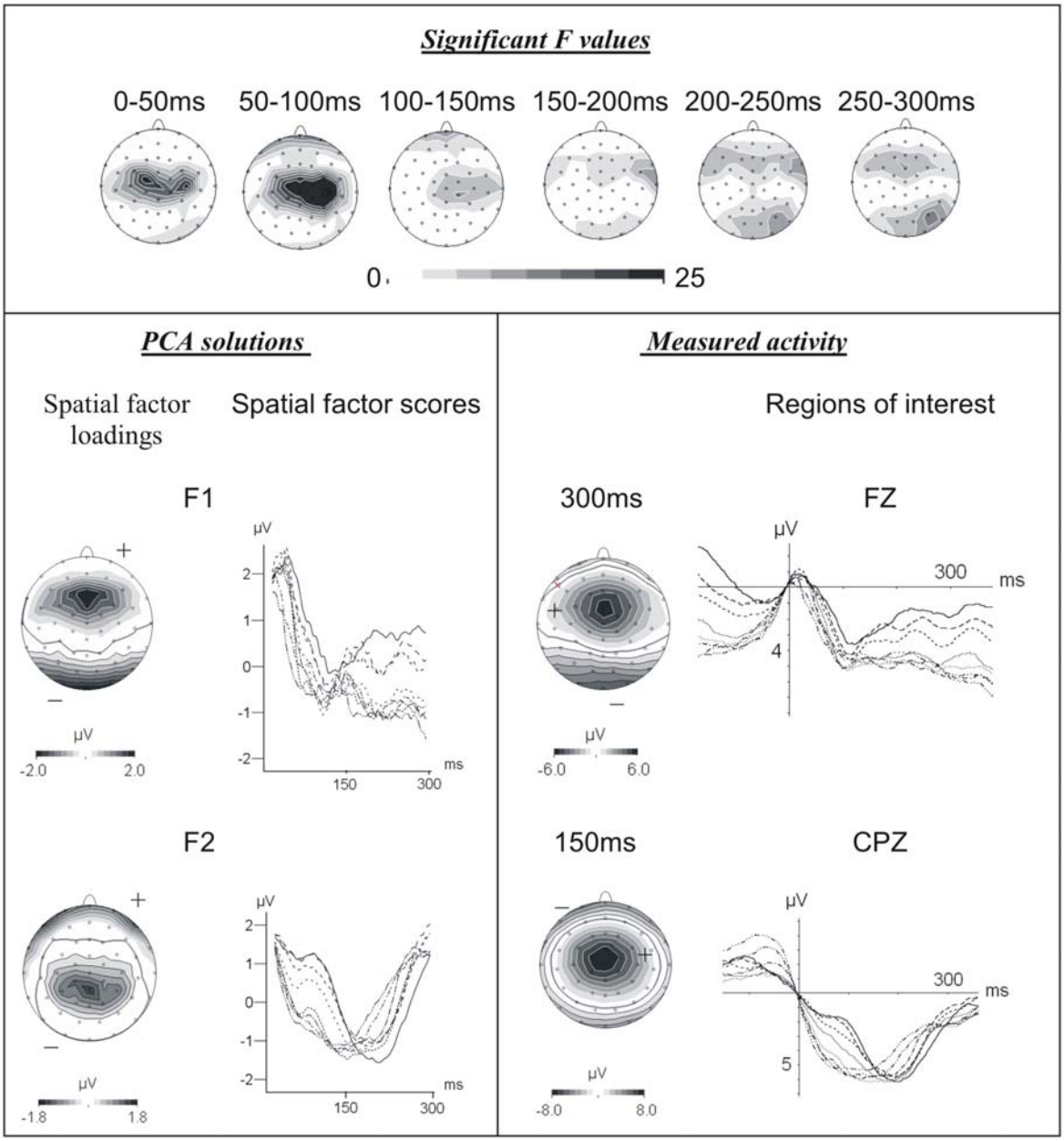

Figure 3-10. *Top:* F values of main factor "distance" at electrodes, where corresponding and corrected P values reached the significance threshold. *Left:* PCA results. *Right:* topography of measured activity at 300 and 150 ms after the stop (average over all delay and distance conditions), as well as ERPs of "electrodes of interest". All time scales are related to the latency of the stop (t=0). The type of line stands for the respective target location condition: 1 2 3 4 5 6 7 8

The component F2 (22%) with a centroparietal-frontopolar topography represents a positive wave, which has a similar topography and time course as the well-known "P3"(see discussion). This deflection can be expected in this time epoch because of the presentation of relevant information required for the encoding. Significant differences between distances around centroparietal sites appeared particularly at the beginning of the epoch. We analyzed this activity at CPZ by a peak to baseline method with a baseline defined from –150 until – 50

ms before the stop and a positive maximum searched between 0 and 300ma in the individual ERPs. Amplitude and the latency of this positive peak entered ANOVAs (with “distance” and “delay” as within subjects factors). A main effect “distance” was found for the latency (F=17,8; P<.001). The grand average waveforms adjusted to the baseline of -150 to 50 ms are shown in Figure 3-11. The mean peak latencies of eight target conditions also depicted in Figure 3-11 show an approximately linear relationship between distances (linear contrast: F = 56,8; P<.001). ANOVA of the amplitude revealed no significant effect (all Ps >.05).

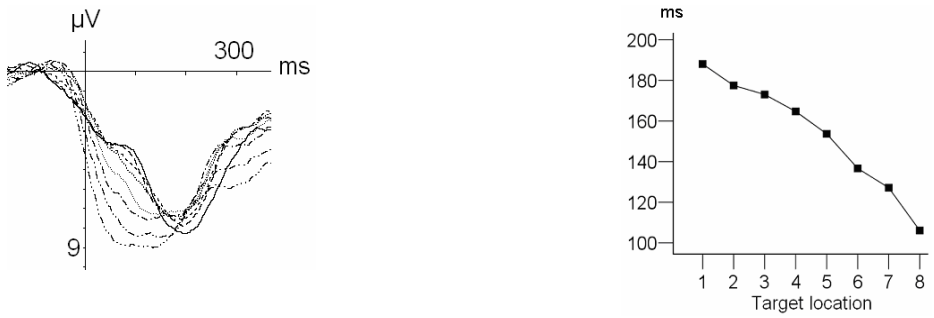

Figure 3-11. *Left:* ERPs of the eight distance conditions at CPZ (average over all delays) adjusted to a baseline of –150 to –50ms in respect to the stop (t=0): 1 2 3 4 5 6 7 8. *Right:* mean latencies of the positive maximum at CPZ.

Discussion

Independent from the type of the sensorimotor transformations involved in the given task, the stop position provided essential information for reproduction. Thus, we expected electrophysiological markers for encoding in this processing phase.

The main differences between conditions revealed by the F-statistic for early time windows were not fully captured by the PCA. The maximal F values of the measured data are arranged along the central electrode row and the dominant ERP activity in the early time range has a maximum at CZ. The spatial PCA, in contrast, extracted F1 with a more frontal and F2 with a more centroparietal topographies. We think that the central differences are associated with a different decline of activity over frontocentral and central electrodes observed in the locating phase (see N4 description in 3.3.2.2).

The second PCA component (F2) was associated with a positive deflection that seems to be closely related to encoding processes. In many tasks, which require classification of events or stimuli into two or more categories, a positive deflection is found, which peaks around 300ms and reaches a maximum over parietal or central areas. The latency of this “classical” P300 component is assumed to be related to the stimulus evaluation time and the difficulty of the categorization of an event (Coles & Rugg, 1995, Coles, Smid, Scheffers, & Otten, 1995,

Fabiani, Gratton, & Coles, 2000). P300 latency increases as categorization becomes more difficult. It is assumed that P300 represents updating of working memory if task relevant, subjectively unexpected events are experienced (Donchin, 1981, Donchin & Coles, 1988). Some studies reported a relationship between the latency of the P300 and the accuracy or latency of an explicit response. In a study of Coles, Gratton, Bashore, Eriksen and Donchin (1985) short P300 latency was associated with higher accuracy, while Kutas, McCarthy and Donchin (1977) reported higher correlation between reaction times and P300 latency, when subjects were given accuracy rather than speed instructions. Despite such dependences, the timing of the P300 is traditionally interpreted as to be independent from response selection and execution mechanisms (Coles et al., 1995).

In the present study mean peak latencies measured at CPZ decreased with an increase in distance. This could suggest a gradual increase in encoding effectiveness with longer distances. This conclusion is in line with our behavioral data, as response variability decreased with increasing of distance in all three delay conditions (see discussion of the behavioral data).

The first PCA component (F1) was associated with distance differences in the late part of the epoch and its topography corresponded rather well with the observed F value distribution. The obtained frontal and frontocentral distance differences may be related to the established error detection and / or monitoring processes associated with activity of anterior cingular regions (see e.g. Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). As mentioned previously, the stop can be assumed to initialize a conflict between afferent and efferent information. A gradual increase in distance in the given experiment was also expected to be expressed in a gradual reduction of this conflict (see behavioral data). Thus, shortly after the stop, some detection and correction mechanisms can be expected, which are occupied stronger in conditions of short movements. Accordingly, the higher amplitude of negative deflections obtained at frontal and frontocentral recording sites in case of short movements may be interpreted as an index of an increase of resources demanding by the error detection / correction mechanisms. The more lateral frontal distance differences may be especially associated with an updating and a correction of initially “wrong” motor plan (aiming a far target), while the rather midline activity may reflect more general monitoring and detection processes, which are often referred to the anterior cingular cortex (see e.g. Gehring & Knight, 2000). The posterior cluster of distance effects is not discussed, since we think that these effects may be contaminated by artifacts resulting from movement breaking.

3.3.2.4 Delay (D)

In order to compare the segments of the three delay conditions with different length we divided each retention interval into three sections of equal length, extending from the end of the backward movement to the reproduction tone. The average amplitude of each segment entered the statistical analyses.

The mean amplitude was affected by both experimental manipulations (delay and distance) in all three time ranges of this processing epoch (see Table 3-5). As shown in Figure 3-12 (top), the different delays caused broadly distributed effects whose topography changed slightly depending on the time window. The factor distance produced much less significant F scores than factor delay. These clusters comprised right frontal and occipital electrodes.

We calculated three separate temporal PCAs for each delay condition in order to identify the main sources of variance[12]. In order to compare the temporal and spatial characteristics of ERPs, we extracted three components in each delay condition, which, taken together, explained most of the total variance: 99% (“0”), 97%(“1”), 97%(“5”).

The time courses of the extracted components (temporal factor loadings) were very similar in all three delay conditions, always comprising a component with high loadings at the beginning and gradually decreasing, a component that peaked in the middle of the delay interval, and a third component that gradually increased towards the end of the interval (see middle part of Figure 3-12). Similar results were obtained in many studies with a CNV paradigm and a constant anticipation interval of 6 seconds (Lutzenberger, Elbert, Rockstroh, & Birbaumer, 1981). The corresponding topographies (temporal factor scores) represent the measured activity used for statistical analyses very well, so we present only the latter in Figure 3-12 . The topographies indicate that there are large differences between delay conditions and only small changes within a delay period. This fact is also reflected in the statistical results (Figure 3-12, top and bottom right).

In order to evaluate the stability of the solutions, we also performed PCAs for individual data. These confirmed the group findings[13].

[12] We changed the sampling rate from 500 to 100Hz, to reduce the amount of data in this epoch. A common PCA could not run due to the different number of data points in the three delay conditions.

[13] This analyses revealed more components in comparison to grand average data, although the factors that explained most of the variance were highly similar with respect to topography and time course.

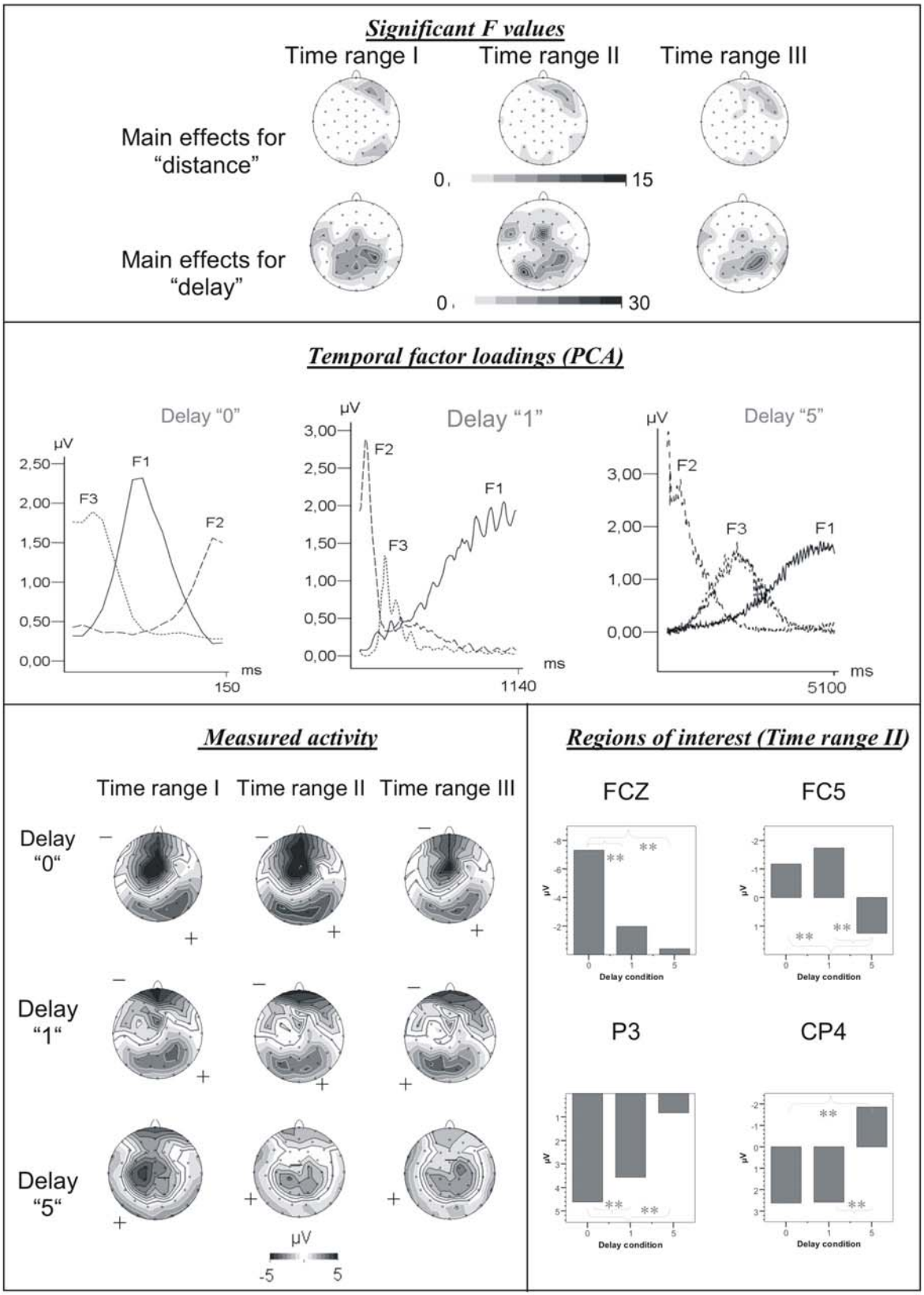

Figure 3-12. *Top:* significant electrode specific F values for "distance" and "delay" main effects. *Middle:* PCA results. *Bottom left:* over distances and time ranges averaged topographies of three delay conditions (see text). *Bottom right:* selective results of post hoc tests for three levels of factor "delay" with respective means at electrodes with the highest F values in the time range II; **P<.01, *P<.05.

Distance effects found in the delay phase were rather weak and difficult to evaluate, because the “delay x distance” and the “electrode x delay x distance” interactions were not significant in the superordinate (“window specific”) analyses (see Appendix 3-G). The relationship between discrete target locations was nonlinear with the most negative values found at the first and the last position (e.g. at AF4 in time range II: quadratic contrast: $F = 29.327$, $P < .001$; Means: -2.94, -1.91, -2.00, -1.83, -1.37, -1.91, -2.29, -3.94 for locations 1, 2, 3, 4, 5, 6, 7, 8).

To reveal more details about processes possibly relevant during the late part of the retention interval (e.g. anticipation, motor preparation), we compared the topographies of the three delay conditions by computing difference potentials. Figure 3-13 shows the voltage maps the third section of the delay interval separately for each delay condition (left) and also the topographies of the difference potentials (right).

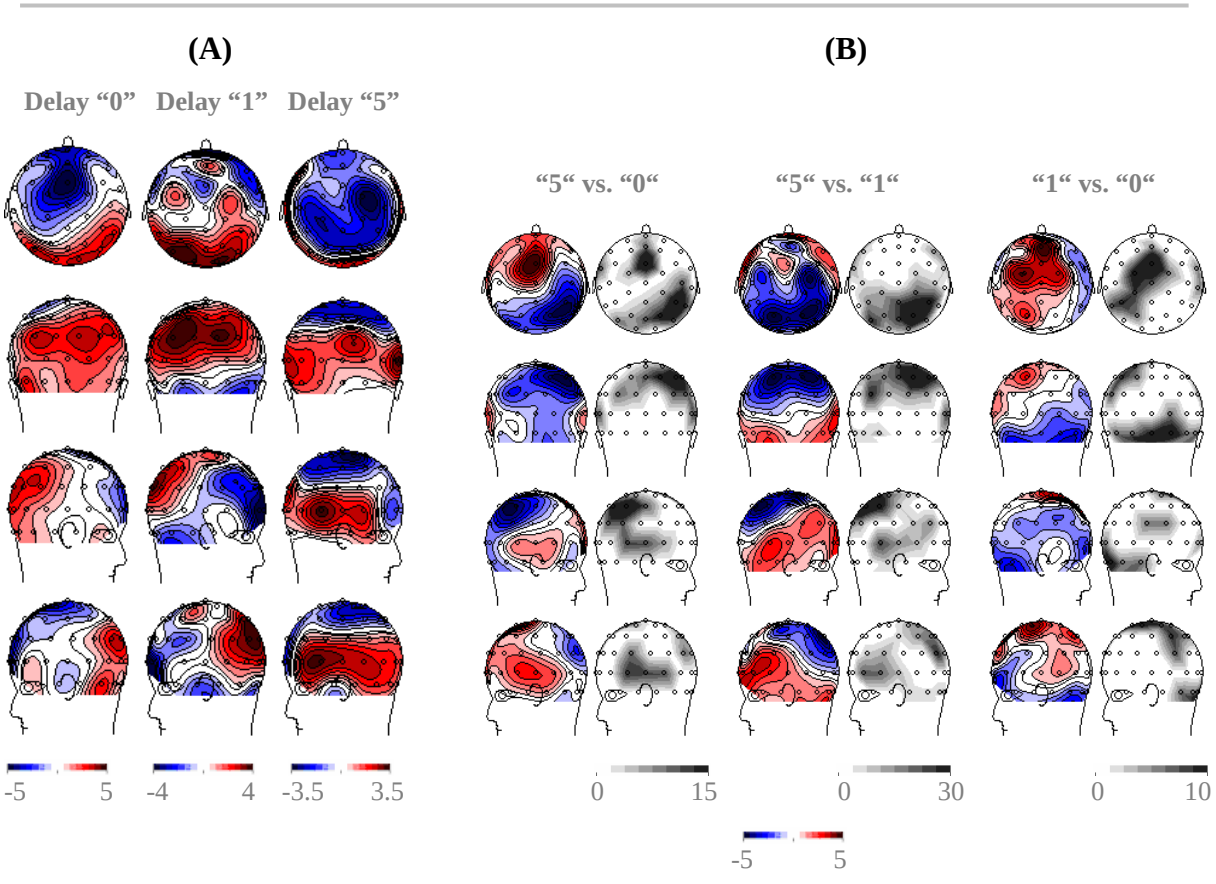

Figure 3-13. (A) Voltage maps of the last third of the retention interval in three delay conditions (µV). (B) Topography of difference potentials (µV) computed for each pair of delay conditions and topographical distributions of according significant F values for factor “delay” computed for each electrode (F value units). All maps are spherically interpolated.

The topography of the shortest delay condition was characterized by negative activity at frontocentral to centroprietal electrodes with a left-hemispheric bias and a maximum at FCZ.

The maximum positivity was present over parietal regions bilaterally. In contrast, the longest delay condition was associated with a broad bilateral negative activity over parietal to frontal locations being maximal at FC2 (right hemisphere). The largest positive amplitudes were found at bilateral inferior frontal to temporal electrode sites. During the late part of the middle delay interval, maximal positive activity was obtained at left parietal recording sites and maximal negativity at central frontopolar electrodes extending to lateral frontal locations. These differences become also evident in the difference topographies and in the maps of significant F values (see Figure 3-13).

The locations of the main differences as well as the dominant activity within each delay condition correspond rather well with the brain regions functionally related to motor tasks (see discussion). The main activity sources seem to be present in premotor and parietal areas around the central sulcus.

Considering relative negativity as a marker of neuronal activation, the main differences between the shortest and the longest delay conditions seem to involve a change of relative hemispheric dominance. In order to test this hypothesis we performed an ANOVA with electrodes FC1 and FC2 as two levels of factor “laterality” and factors “distance” and “delay”. The corresponding ERPs and the results are shown in Figures 3-14, 3-15 and Table 3-6.

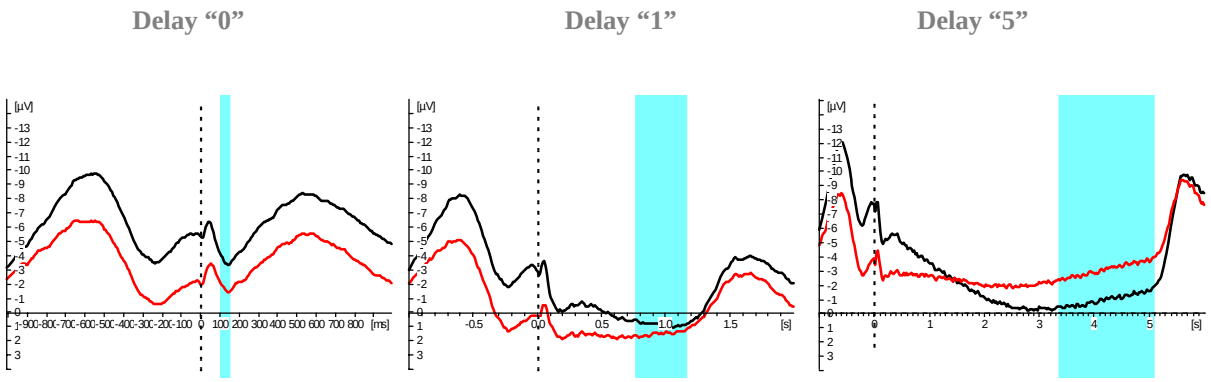

Figure 3-14. ERPs measured in three delay conditions at FC1 (black) and FC2 (red). Vertical dashed line reflects the end of the first backward movement and marked segments show the time-range chosen for statistical analyses (i.e. last third of the retention interval).

As shown, the stronger activity at frontocentral locations over the contralateral hemisphere in respect to the moving hand is present in the shortest delay condition. This asymmetry seems to decrease, when the delay is prolonged to 1 second. During the longest delay condition the ERPs crossed at about 1.5 seconds and the ipsilateral activity became stronger than that measured at the homologous location of the left hemisphere. The critical “laterality x delay” interaction was significant (see Table 3-6 for statistical results and Figure 3-15 for means).

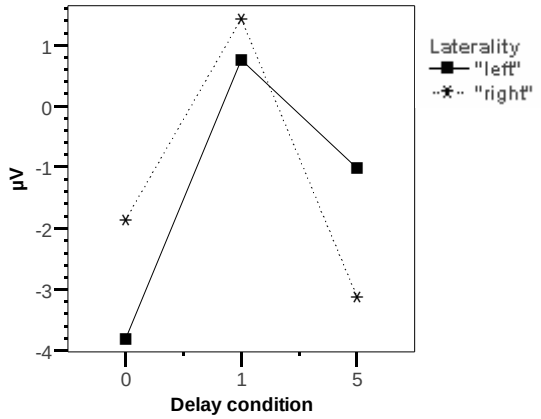

Figure 3-15. Mean voltage values at FC1("left") and FC2 ("right") in the time range III of the retention interval.

Table 3-6. Statistical results performed with the mean amplitude of ERPs at FC1 and FC2 in the last third of the delay phase. Degrees of freedom were corrected according to Huynh and Feldt (1976), when sphericity assumption was violated

Effect	df	F	P
"laterality"	1,17	.10	.754
"delay"	2,34	**5.22***	**.011**
"distance"	7,119	2.23	.050
"laterality & delay"	2,34	**5.68****	**.007**
"laterality & distance"	7,119	**2.42***	**.027**
"delay & distance"	14,238	1.77	.078
"laterality & delay & distance"	14,238	1.28	.257

The results of this analysis suggest that the negative activity over premotor areas was stronger in the left than in the right hemisphere, when the delay was short ("0"), and stronger in the right that in the left hemisphere, when the delay was long ("5").

The scalp distributions allow only restricted conclusions about the nature of the neuronal generators. In order to delineate, whether "quantitative" or "qualitative" factors may have caused the observed delay effects, we performed a source analysis. We were interested in activity preceding the reproduction tone that could reflect processes related to motor preparation. Hence, we again used the third part of the retention interval for this analysis. Initially, the sampling rate of the middle and the long delay conditions was changed to 50 and 10 Hz respectively, to circumvent limitations of the software. LORETA current source densities were then calculated for each experimental condition (24: 3(delay) x 8 (distance)) and each data point (Number of data points: delay "0" = 25, delay "1"=19, delay "5" = 17). Subsequently, LORETAs were averaged over all time points and distance conditions according to the three delays. These results are shown in Figure 3-16 and Table 3-7.
The generator constellation was similar in all delay conditions, including several frontal areas (BA6, 8, 9) and the left inferior parietal region (BA 40). However, the main current density maxima had a clearly different distribution in the three conditions. The activity of the shortest

Table 3-7. LORETA current density of local maxima with activity extended 2.6x10^-2, 6.4x10^-2 and 2.4x10^-2 (μA) for delay "0", "1" and "5" respectively.

Delay condition	Anatomical area	Brodmann Area	Talairach coordinates X	Y	Z	Current density (μA)
	Middle Frontal Gyrus	9	-31	31	43	4.97
	Superior Frontal Gyrus	8	4	17	57	3.56
	Superior Frontal Gyrus	8	32	17	57	3.51
"0"	Precentral Gyrus	9	39	24	43	3.27
	Middle Frontal Gyrus	8	25	31	43	3.17
	Superior Frontal Gyrus	6	-3	-4	71	3.08
	Middle Temporal Gyrus	37	-52	-60	-13	2.92
	Inferior Parietal Lobule	40	-38	-46	50	2.78
	Middle Frontal Gyrus	6	32	3	57	9.63
	Superior Frontal Gyrus	6	-24	3	57	9.55
	Medial Frontal Gyrus	8	-3	38	43	8.95
	Middle Frontal Gyrus	6	-45	3	50	7.59
"1"	Inferior Parietal Lobule	40	-45	-39	50	7.51
	Orbital Gyrus	11	-3	45	-20	6.83
	Medial Frontal Gyrus	10	4	59	-6	6.72
	Medial Frontal Gyrus	10	-3	59	-6	6.72
	Middle Frontal Gyrus	9	-31	31	43	6.46
	Superior Frontal Gyrus	6	25	3	57	4.63
	Inferior Parietal Lobule	40	-38	-46	50	3.11
	Precuneus	7	4	-74	36	2.94
	Medial Frontal Gyrus	6	-3	-32	64	2.87
"5"	Precuneus	19	32	-74	43	2.87
	Middle Frontal Gyrus	9	-31	31	43	2.85
	Medial Frontal Gyrus	6	-24	-4	57	2.71
	Middle Frontal Gyrus	6	-45	3	50	2.67
	Postcentral Gyrus	7	18	-53	71	2.47

delay was concentrated in the left middle frontal gyrus (BA9). In the middle delay condition the activation was bilateral within the middle frontal gyrus (BA6), and in the longest delay condition the sources indicate again the activation of the middle frontal gyrus, but now the current flow is asymmetric being higher in the right hemisphere. These results suggest substantial differences between the conditions. There is in particular a different involvement of the two hemispheres with changing delay epochs: A left hemisphere activation with a very short delay, and a right hemisphere activation with a long delay.

While the shortest delay condition was associated with phasic deflections, the ERPs of the middle and the long delay intervals had a more tonic characteristic DC-like potentials. It is worth mentioning that both conditions differed not only in mean evoked activity and in the source configuration, but also in the polarity at locations, which were responsible for the dynamic amplitude changes preceding the reproduction tone. The PCA results suggested similar dynamics across all delay conditions, when the retention intervals were considered as a whole.

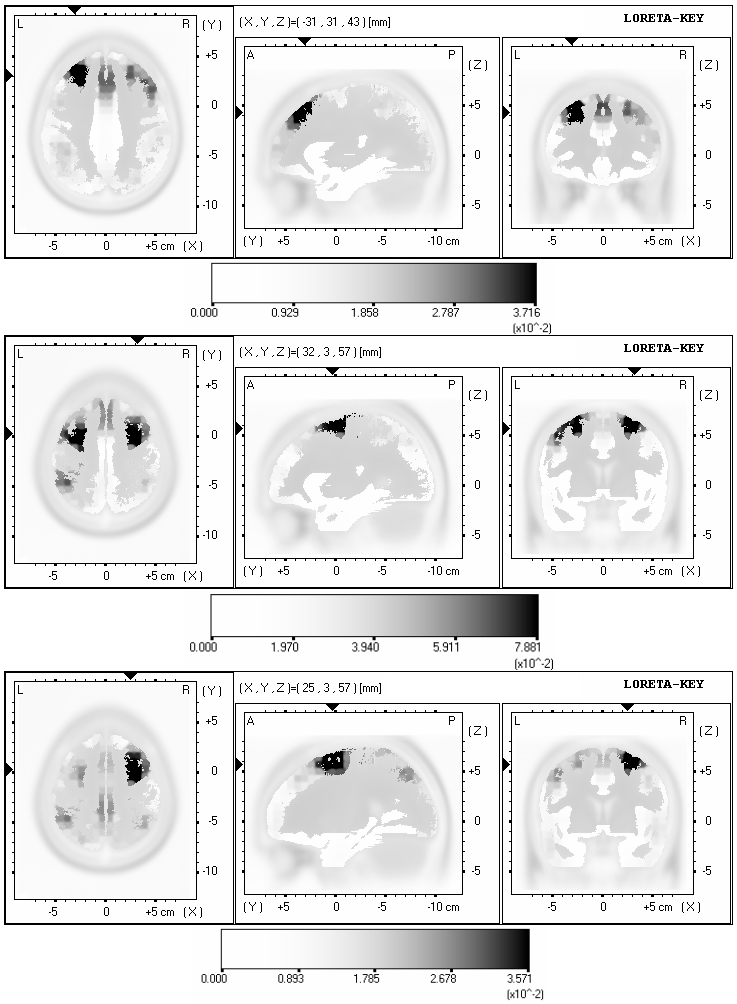

Figure 3-16. LORETA current density distribution in three delay conditions. Activity is color-coded, with maximum corresponding to black and zero to white. The tomographies consist of axial, sagittal and coronal slices through the respective point of maximum activity as indicated by X, Y and Z coordinates in Talairach space.

As shown in Figure 3-17 “decreasing” and “increasing” activity patterns are clearly detectible in both delay conditions. However, the electrode locations sensitive to these changes seem to be different dependent on delay. The positive going waves, preceding the reproduction phase are mainly localized at left posterior recording sites during the middle retention interval (labeled as PSWs in Figure 3-17). The negative going activity (NSWs) is visible over right anterior regions in this condition. Although the topography of the “increasing” negative slow waves occurring during the late part of the longest delay interval seem to overlap the corresponding activity of the middle delay condition (see e.g. FC4 in Figure 3-17), it seems to be restricted to the frontrocentral array of electrode locations. The increasing positive activity was mainly obtained over left frontal areas and right temporal regions. These observations suggest that not only mean activity patterns, but also processes associated with a local “increasing” and “decreasing” of excitation during the late part of the retention interval differ between the two longer delay conditions.

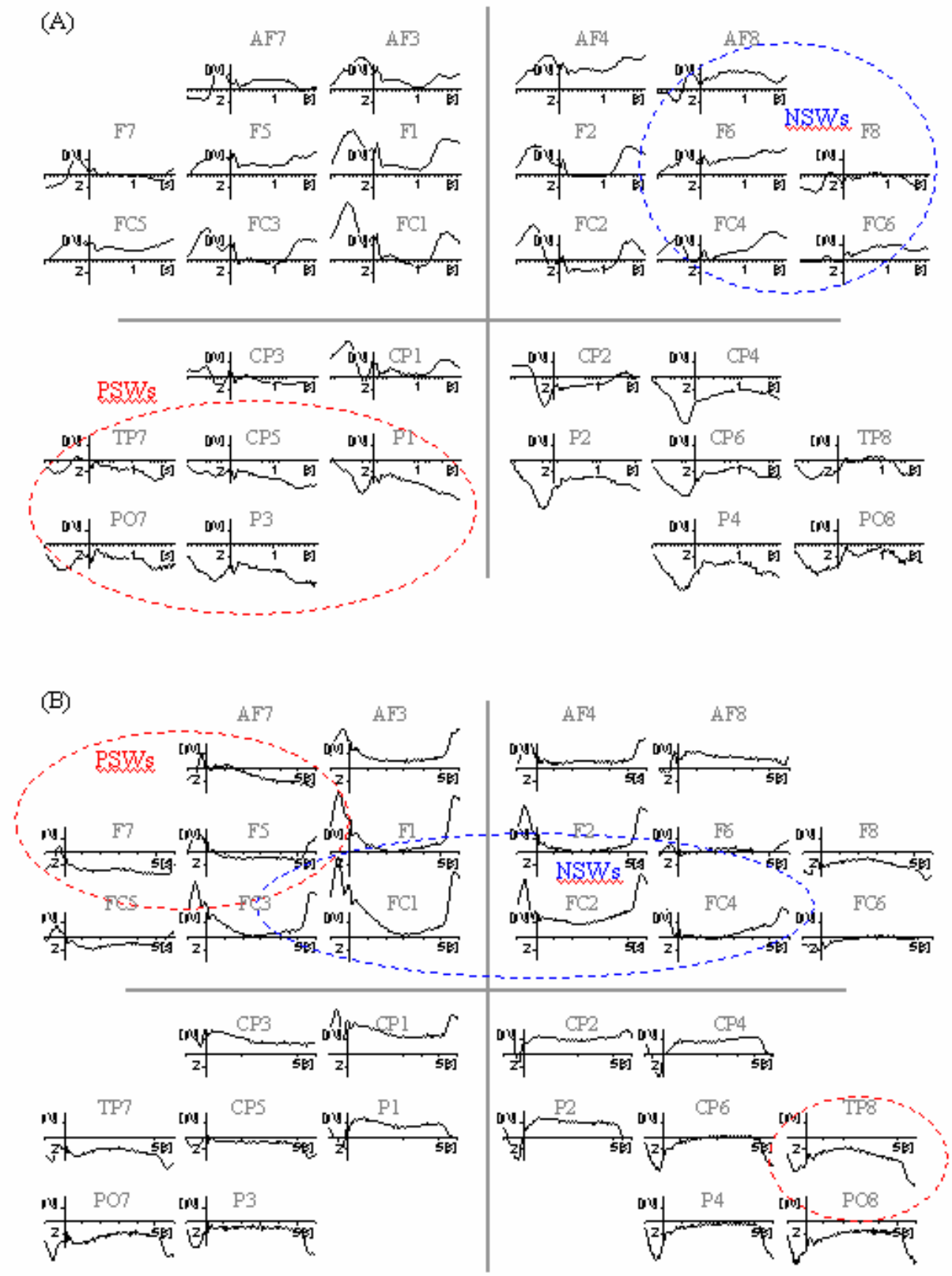

Figure 3-17. Evoked activity of the delay phase in the delay "1" (A) and delay "5" (B) conditions. ERPs were synchronized to the offset of the first backward movement and baseline corrected according to the –2000-1000 ms interval in respect to the first imperative Go-signal. Note: only selected electrodes are shown (not shown are central, midline and outer arrays as well as occipital locations). Some "locations of interest" are marked (see text). PSWs = positive slow waves, NSW = negative slow waves.

Discussion

The PCA of the ERPs in the delay period revealed strong similarities of the temporal dynamics of the slow potentials despite different durations (see Fig. 3-12). However, the topography differed for the three delay conditions and was also to some extent dependent on the time range.

The delay processing phase in the present study is similar to a typical CNV ("Contingent Negative Variation") paradigm. A typical CNV task involves a presentation of pairs of stimuli, separated by a time interval. The first warning signal provides information about a second stimulus (imperative stimulus) that requires a response. During the foreperiod of this reaction time task, a slow negative wave develops, firstly described by Walter and colleagues (1964). This deflection was initially interpreted as "expectancy wave", but further research showed that it is composed of at least two components, called "O-wave" (for orientation) and "E-wave" (for expectancy) (Loveless & Sanford, 1974). The early "O-wave" proved to be sensitive to characteristics of the first stimulus (e.g. to its modality, intensity, and duration) and was therefore assumed to be a type of an orientation response. The functional role of the late component is still controversial (Fabiani et al., 2000; Brunia & Van Boxtel, 2000). It was suggested, that the "E-wave" is the readiness potential, observed in voluntary self-paced movements (e.g. Rohrbaugh & Gaillard, 1983). Others have argued that there are also nonmotoric E-waves (e.g. Van Boxtel & Brunia, 1994). The existence of both components was obtained with different durations of the foreperiod, including 1 second (e.g. McCarthy & Donchin, 1978). Moreover, by comparing the PCA results of seven studies, Lutzenberger et al. (1981) could show that with a constant foreperiod of 6 seconds, an intermediate component appears in addition to the early and the late components.

Although the task of the present study resembles the CNV paradigm to some extent, it can be assumed that the motor matching task may include more and possibly other processes than a simple cued reaction time task.

The CNV is a phenomenon that belongs to the category of slowly changing cortical potentials, which were shown to be closely related to cognitive processing. There is a considerable body of empirical evidence, suggesting that the topography of slow event related potentials depends on the type of information processed in a task (for review see Rösler, Heil, & Röder, 1997). Moreover, slow waves can indicate different stages of computation, as encoding, transformation or maintaining of information, which are observable as distinct deflections in time and space.

Following this, our results suggest that the motor or spatial information processing steps are similar in all delay conditions due to the highly comparable temporal dynamics of the slow wave patterns. On the other hand, different topographies indicate differences in generator constellations in the three retention periods.

A key question is, of course, whether the results from ERP segments of different length are comparable. Our analyses rest on the assumption that temporal and functional processing requirements should be similar irrespective of the delay, because the same physical stimuli were used and the motor requirements were the same. We assume that the basic sequence of processing steps should be the same and the PCA results seem to support the validity of this assumption. However, there are some caveats:

Firstly, similar dynamics may result from the statistical properties of PCA. It extracts DC components first, because they "naturally" bind more variance as compared to high frequency components.

Secondly, the extracted factors may not reflect components of the same frequency range. While in the delay "1" and delay "5" condition the ERPs are in the slow wave range, the ERPs in the short delay condition have a more phasic characteristic and may represent a different type of generator.

Having these caveats in mind, the conclusion that the same sequence of processes is triggered in all three delay conditions is, of course, tentative. All the more as the topographies are distinct, which suggests that, most likely, different neuron populations are activated in the three delay conditions (see also below). To integrate both aspects would mean that similar micro processes are triggered with equivalent time courses but within distinct cortical areas.

The spatial information derived from ERP topographies and from the source analysis may provide some insight into where the involved generators are approximately located. Motor activity involves many brain areas, including parietal, frontal and subcortical structures (see e.g. Grafton, Hari, & Salenius, 2000). Moreover, task-related information required for the planning and the execution of movements to visual targets is integrated within distinct parietofrontal networks (for review see e.g. Wise, Boussaoud, Johnson, & Caminity, 1997, Burnod et al., 1999, Matelli & Luppino, 2001). The representations of limb positions, target locations and potential motor actions are attributed to parietal regions, while executive processes, like planning, selection and execution of motor acts are functionally related to the precentral cortical areas (e.g. Kalaska, Scott, Cisek, & Sergio, 1997, de Lange, Hagoort, & Toni, 2005).

Compared the visuomotor domain there is much less knowledge available about the neurobiology of purely kinesthetic tasks. By using PET (Positron Emmision Tomography) in a kinesthetic task, Butler et al. (2004) identified a similar neuronal network (premotor-parietal-cerebelar circuit with right hemispherical dominance) that was previously reported in several visuospatial tasks. The authors argued for similarities of kinesthetic and visual spatial information processing.

When the delay interval was long ("5") negative waves of a high amplitude were obtained over frontocentral to parietal locations, with a maximum at a right frontocentral electrode (FC2). The performed source analysis indicated a strong activity cluster within the right superior frontal gyrus, which lay approximately under the mentioned electrode (FC2). Further areas in the parietal and frontal cortex also showed high current densities suggesting their contribution to the activity measured at the scalp.

Negative deflections with a similar topography preceding and following a motor act are reported by Wheaton, Shibasaki and Hallett (2005). The authors investigated self-paced praxis movements and discussed the mentioned results in the framework of functional coupling of premotor and parietal areas.

The dominant activity during the middle delay interval ("1") was characterized by positive deflections over inferior parietal regions and by negative activity at frontopolar to frontocentral regions. By investigating the relation between spatial attention and motor intention for hand movements, Praamstra, Boutsen and Humphreys (2005) obtained a similar topography in the time window of P300 after a cue indicating either a response hand or the location of the target presented one second after. These results were related to a "frontoparietal attentional network", identified previously in several neuroimaging studies (e.g. Corbetta & Shulman, 2002) and its relation to motor preparation processes was emphasized. Our source analysis also suggests that premotor-parietal areas contributed strongly to the measured evoked activity indicating a special role of the left inferior parietal regions.

Although the empirical basis for a straightforward interpretation is still very limited our results suggest that the retention of movement information and motor preparation in the delay "1" and delay "5" conditions are functionally associated with the activity in premotor-parietal networks. Moreover, a careful visual inspection of the ERP topographies suggested that despite the polarity characteristics (see below), the involved networks may be "qualitatively" different. The posterior activity seems to be the result of different sources depending on the delay. While the negativity observed during the longest delay interval is primarily distributed

over *superior* parietal areas the positivity in the middle delay condition has its focus over *inferior* parietal regions. This observation also seems to be supported by the source analysis, which indicated activity clusters in superior areas (BA7) in the delay "5" condition additional to the inferior sources (BA40). The latter were present in both delay conditions. Similarly, frontal negative slow waves were obtained over dorsal premotor areas, when the delay was long ("5") and over more ventral regions, when the delay had medium length ("1"). The most active sources within parietal and frontal areas also showed a slight drift towards more ventral locations when the delay increased from one to five seconds (this was true for the right frontal and the left parietal locations, see Table 3-7). If these observations are valid, the results would indicate some functional differences between both delay conditions that are possibly related to functional specializations within parietal and premotor areas along a ventral-dorsal gradient (e.g. Matteli & Luppino, 2001, Rizzolatti & Matelly, 2003, Burnod et al. 1999, Schubotz & von Cramon, 2003).

In addition to the similarities of the temporal dynamics and the topographical differences, the polarity characteristics of the slow waves are also noteworthy. The locations showing "positive" and "negative" going waves during the late part of the retention interval differed substantially dependent on the delay. Negative slow waves are assumed to be associated with enhanced excitability, while positive slow waves indicate a disfacilitatory state in the area under the electrode (see e.g. Birbaumer, Elbert, Canavan, & Rockstroh, 1990, Schupp, Lutzenberger, Rau, & Birbaumer, Hinterberger et al., 2003). Accordingly, the functional role of the negative slow waves is seen in "active" processes as an allocation of "resources" to cortical processing modules (Rösler et al., 1997). The decreased brain activity expressed in positive deflections may result from an active inhibition or simply from a reduced postsynaptic activity. Their functional role seems to be much more complex and is still not fully understood (e.g. Birbaumer, 1999). Nevertheless, positive and negative slow cortical potentials seem to reflect at least two distinct neuronal mechanisms ("activation" vs. "deactivation" or "inhibition"). By following this argument our results seem to indicate that not only distinct neuronal networks may be involved (see above), but also different functional mechanisms of retention of information and motor planning may take place dependent on the time of response.

The phasic activity in the shortest delay condition was associated with a topography that is often obtained during movement preparation and execution in simple motor tasks. The main

cluster of negative activity was obtained at frontocentral locations and at further electrodes located primarily over left sensorimotor areas, suggesting the involvement of SMA and the contralateral sensorimotor cortices as possible sources. This result agrees with findings reported by Darling, Seitz, Peltier, Tellman and Butler (2006). Using a short delay in a kinesthetic matching task, the authors obtained the dominant activity in regions localized closely to the sensorimotor cortex within the hemisphere contralateral to the moving hand[14]. Moreover, the negative ERPs over the SMA and sensorimotor areas, which are usually more pronounced over the hemisphere contralateral to the used effector, is a typical finding, when planning and execution of simple self-paced repetitive movements are investigated (i.e. within the readiness potential paradigm; Deecke et al., 1999, Cui, Huter, et al., 2000, Ball et al., 1999, Babilony et al., 1999).

Since the current interval between the end of the first backward movement and the second imperative Go-signal was very short (delay "0"), the obtained activity may simply be related to the "reverberation" of the networks, which were previously active. On the other hand, the brain may "actively" maintain the activity in these areas and, thus, provide a transient storage of relevant information about the encoding movement. In any case, these processes would differ from those obtained under two other conditions.

However, the performed source analysis seems to fit only partly in the last mentioned results. Although the left hemispheric dominance and SMA activation was observed, the clusters of maximal current density were localized in more anterior areas in respect to the electrode, which showed maximal negative amplitudes.

If the late range of the retention interval may be related to certain aspects of planning or motor preparation, in which especially premotor areas are involved, one obvious difference between the shortest and the longest delay conditions would consist in a hemispheric shift of dominant activity from the left (delay "0") to the right (delay "5") hemisphere. This is an interesting observation, since movements were performed with the right hand and the encoding situation was highly comparable in all delay conditions. The right hemisphere is traditionally assumed to be associated with global, spatial and extrapersonal aspects of information processing, while the left hemisphere has been related to local, internal and dynamic features of motor control (see e.g. Serrien et a., 2006 for a review). In light of this discussion, our results suggest that preparation after a long delay (5) would include global, spatial and / or static aspects of an upcoming movement (e.g. movement end position), while a direct reproduction would be based on local, perceptual and dynamic information (e.g. movement trajectory).

[14] The authors used PET and compared conditions, in which the right or the left hand was used for target localization and reproduction movements.

These conclusions would fit well in the results of the behavioral analyses (see also General discussion).
It is worth mentioning that the topography of the shortest delay condition conforms quite well to the activation pattern, obtained at planning simple finger movements, which were externally triggered (Jahanshahi et al., 1995, Jenkins et al., 2000). On the contrary, planning of self initiated movement was associated with activity clusters within bilateral premotor and parietal areas, which seem to be compatible with the topographies of both other delay conditions ("1" and "5"). This fact may highlight some further processing features, which may differ between delay conditions.
In summary, preparatory activity preceding the imperative signal for reproduction differed significantly depending on the delay condition, as expressed in different ERPs topographies. These differences may reflect different neuronal substrates and / or different functional mechanisms underlying the retention of information and motor planning.

3.3.2.5 Motor programming (MP)

The mean amplitudes measured after the reproduction tone yielded significant delay effects in all measurement intervals (see Table 3-5, section MP). The electrode specific effects showed that the main differences between the delay phases arose in the late range of the epoch over frontocentral regions (see Figure 3-18, top).
The temporal PCAs performed in this processing epoch revealed seven components, whose temporal factor loadings are shown in Figure 3-18 (middle).
The component F1, which accounted for most of the variance (87%) had a topography with the frontocentral maximum in all delay conditions and an increasing, biphasic negative time course. We defined the electrode FCZ as a region of interest (Figure 3-18, bottom right) and analyzed its activity by using a peak to baseline method. The negative maximum around 300 ms was determined in the individual averaged potentials and two separate ANOVAs were run with the latency and the amplitude of this peak. These analyses revealed a significant main effect of factor "delay" for latencies as well as for amplitudes (Latency: $F=15.6$, $P<.01$; Amplitude: $F=64.8$, $P<.001$). The mean values of each delay condition are shown in Figure 3-19. Post hoc comparisons indicated that all means differ significantly from each other (all $P<.05$), suggesting a longer peak latency and a larger peak amplitude with longer delays.

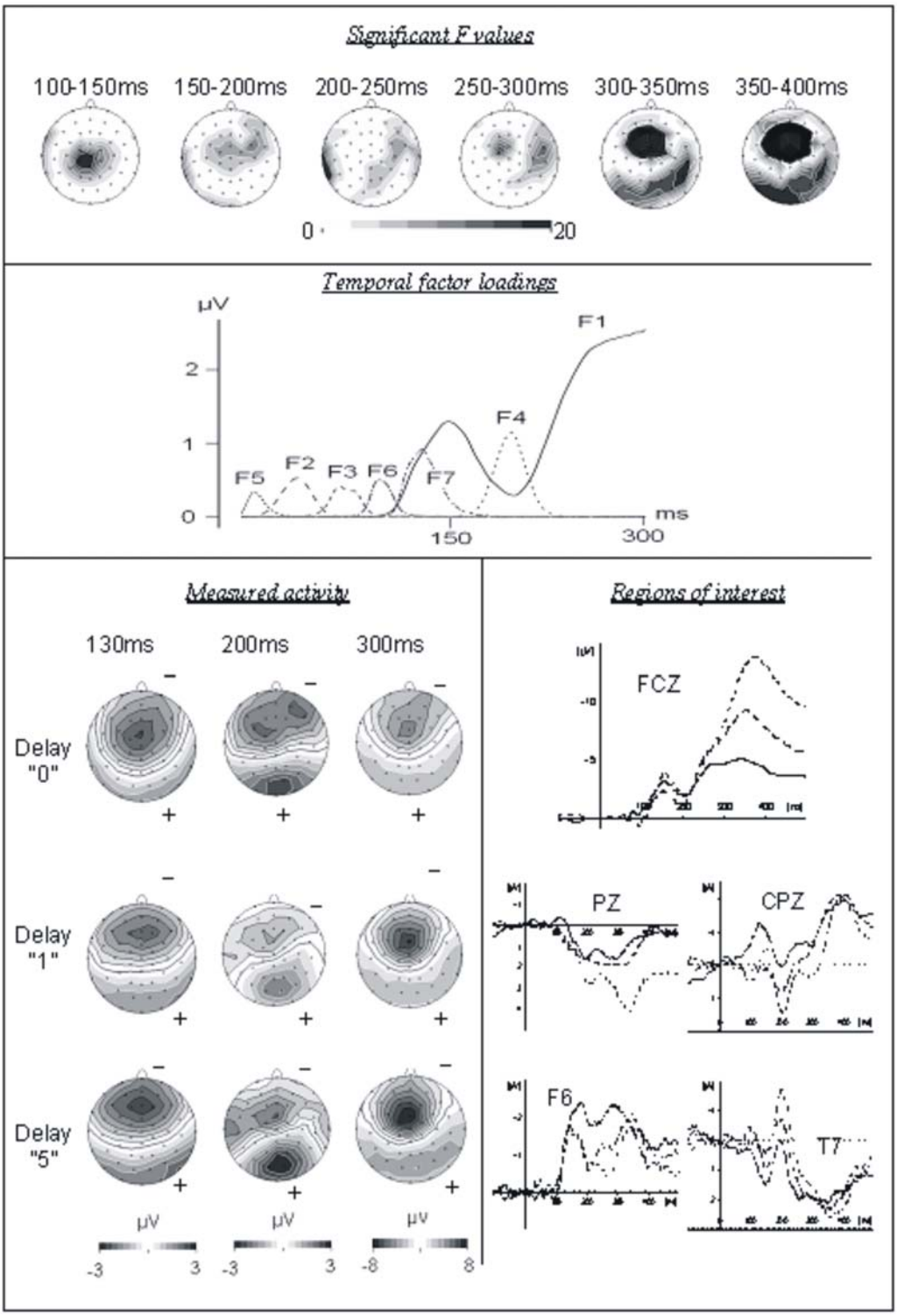

Figure 3-18. *Top* : F values at electrodes revealed a significant main effect "distance". *Middle:* PCA results. *Bottom left:* measured activity of three delay conditions at chosen time points (*left*) and at chosen electrode locations (*right*); —— delay "0", - - - delay "1", ... delay "5". Note: all time scales are adjusted to the reproduction tone (t=0).

Moreover, strong delay differences were also obtained over parietal regions in the late range of the current processing epoch. The ERPs of the long delay condition ("5") were characterized by a positive deflection, which seems to be absent in both other conditions. Post

hoc tests at PZ in the time window between 300 and 350 ms indicated that the longest delay condition differed significantly from both others (Ps = .001).

The activity around 200ms after the tone seems represented by factor F4 and has a different topography in the three delay conditions. The shortest delay condition shows a stronger right frontal negativity (post hoc test at F6 in 150-200ms time range: 0vs1, P<.01; 0vs5, P<.01). In contrast, in the delay "5" condition more activity is present at temporal sites than in the two shorter delays (e.g. all conditions differed significantly from each other at electrode T7 in the 200-250ms time-window, Ps <.05).

In an early time range (100-150ms), in which the PCA extracted three further components (F3, F6, F7), the main cluster of delay effects was found at centroparietal electrodes. At these sites the short delay condition ("0") was associated with higher negative activity than the two others (Post hoc tests at CPZ showed that all conditions were significantly different from each other, P<.05).

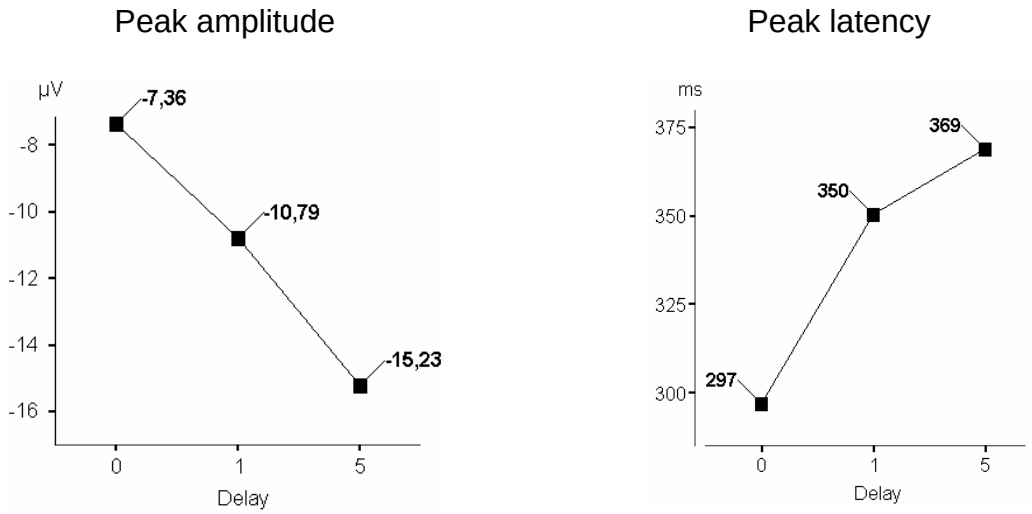

Figure 3-19. Means of peak amplitude and peak latency at FCZ as function of delay condition (see text).

Discussion

Based on an extensive review of ERP literature, Brunia and van Boxtel (2000) postulated three processes to be involved in the initiation of voluntary self-paced motor acts. Selection mechanisms to be reflected in RP1 (readiness potential 1), are assumed to be associated with SMA (supplementary motor area) and basal ganglia activity. Context dependent parameter setting is considered to be expressed in RP2 (asymmetric part of readiness potential), in which the cerebellum and the primary motor cortex are involved. The command to move seems to be associated with a discharge of pyramidal tract neurons in the primary motor cortex and is assumed to be reflected in the MP (motor potential).

Although this model is based on results found with the readiness potential paradigm, we use it as a heuristic in order to classify our findings. It can be assumed that shortly before response onset, corticospinal outflow must become manifest as a negative deflection over central electrodes. And indeed, similar to the MP we measured a comparable component in all three delay conditions. Moreover, the maximum F values were observed over frontocentral and central areas at the end of the epoch. Although the distribution of the F-values at these sites as well as the topography of the measured negativity before movement onset had a slightly left oriented distribution, the largest amplitude values were found at FCZ, indicating a stronger involvement of SMA rather than MI (for similar results see Deecke et al., 1999). The increase in the negative amplitude over frontocentral electrodes in the longer delay conditions could be due to different amounts of determining the motor command. One may speculate that if a movement was performed shortly before reproduction, the involved motor cortices may be still in an active state (see also discussion of the delay interval). Thus, a "reactivation" of these areas may be "easier", because the critical threshold can be achieved faster than if the interval between successive movements is long. This assumption seems to be partly supported by the ERPs of the retention interval.

Strong delay effects were also found over parietal electrodes at the end of the epoch. The long delay condition was associated with a stronger positive activity as the two others that was broadly distributed. In the readiness potential paradigm such positive deflections are also obtained and are labeled as P1 (Brunia, 1987). Their role still does not seem to be clear. In the current experiment, we assume that this positive deflection may be related to recall processes from short-term memory. In another study, in which visuomotor processes were investigated, we obtained similar results. Posterior ERPs measured after a reproduction tone showed a pronounced positive deflection, when the reproduction tone occurred after 5 seconds. This deflection was not obtained in the two shorter delay conditions ("200ms" and "1000ms"). Comparable results were previously reported by Reinvang, Magnussen, Greenlee and Larsson (1998).

As mentioned above, context dependent parameter setting for an upcoming movement was related to RP2. We obtained several phasic waves in an early time range, which may be associated with this component and the ascribed function. The largest delay effects were found at centroparietal locations, at which the ERPs of the short delay condition showed a higher negative amplitude then both others. These results may suggest that the regions lying under these locations (most likely primary somatosensory cortex and superior parietal areas)

are strongly involved in the programming processes (parameter setting, trajectory formation etc.) and / or recall in the short delay condition ("0") as compared with both others.
In the middle time range (about 200ms) strong differences between delay conditions were found over temporal areas. An increase in delay was expressed in an increase in phasic activity at these sites. This result may reflect an increasing involvement of temporal regions in motor planning / recall processes with delay.

3.3.2.6 Reproduction movement (RM)

Distance effects

In the reproduction phase the topography and the timing of significant effects were very similar to those of the first movement (see Table 3-5, Figures 3-8 and 3-20). Significant differences between the movements of different length occurred at first at left centroparietal and frontopolar sites (from 100-150ms) and drifted then towards frontocentral sites. The ERPs of different target conditions differed less than during the encoding movement probably because of higher movement variability.
By using spatial PCAs we identified two stable components, which had very similar wave courses and topographies to those of the locating phase (see Figures 3-8 and 3-20). We included all delay conditions in this analysis because the interactions between the factors "distance" and "delay" were not significant.
The second component (F2) that reflects activity over frontocentral cortex shows an amplitude and latency modulation similar to that obtained in the locating phase. Post hoc tests at FCZ in the time window 250-300ms indicated a highly significant linear contrast ($F= 22,3$; $P<.001$) due to a gradual increase in relative negativity (if the time range about 150 ms is considered as reference) with increasing distances to be moved (see Figure 3-20).

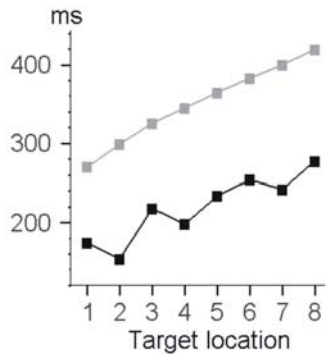

Figure 3-21. Latency of the negative peak at FCZ in the grand average (–■–) and averaged movement duration until the endpoint (–■–).

Unfortunately, due to much noise, a peak detection was not possible for the frontocentral peak (at FCZ). In order to show its relation to movement duration, we selected the negative maxima in the time range 150-350ms from the grand average potentials and the movement times and put them in one graph (see Figure 3-21).

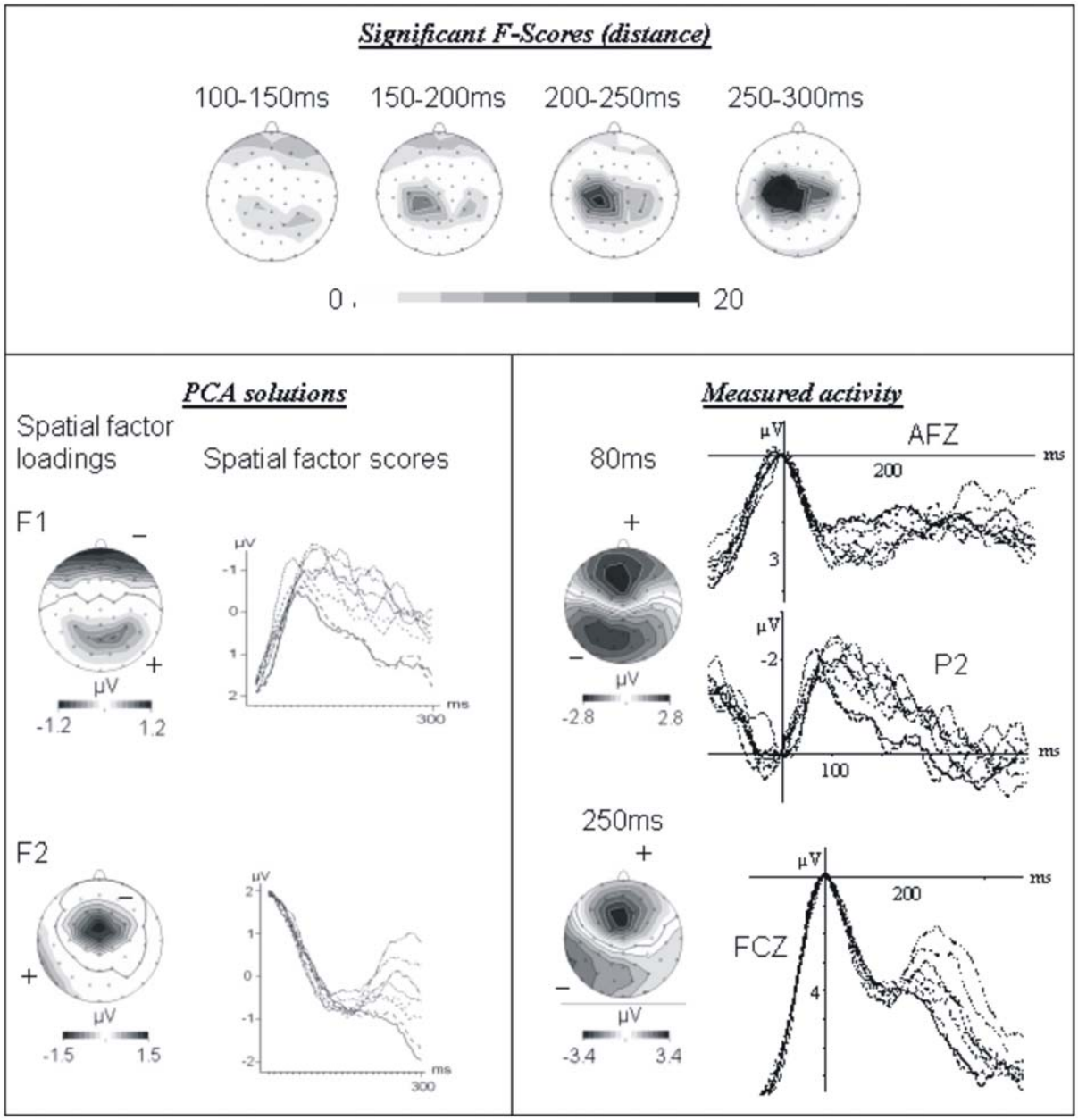

Figure 3-20. *top*: F values of main effect "distance" at electrodes, where corresponding P values became significant. *left*: PCA results; *right*: topography of ERPs at 80 and at 250ms (average over all delay and distance conditions) after the movement onset and ERPs of 8 distance conditions synchronized to the movement onset (t=0) at electrodes P2 and FCZ with follow line assignment:

1 2 3 4 5 6 7 8

The peak latency and the movement time show an almost parallel increase with increasing distance. This is in contrast to the encoding phase, in which both variables showed an increasing deviation from each other with increasing distance. Moreover, both variables now show a larger offset (132ms) than during the first movement (27ms, see Figure 3-9). These relations suggest that a process, which is represented by the frontocentral activity at this time range, takes place between 150 after the movement onset (approximate onset of the negative

going waves) and about 120 ms before the movement endpoint (approximate latency of the negative peak) and seems to be distance specific due to the amplitude modulation.
The variance of evoked activity over frontopolar and parietal electrodes was bound by the component F1. The distance effects at these sites were less pronounced, but the main effects and the respective linear contrasts often became significant (e.g. linear contrast for the150-200ms time window at P2 - P=.001 and at AFZ - P= <.001), suggesting a trend towards a higher negative amplitude with an increase in distance at parietal and anterior frontal sites (see Figure 3-22 for means).

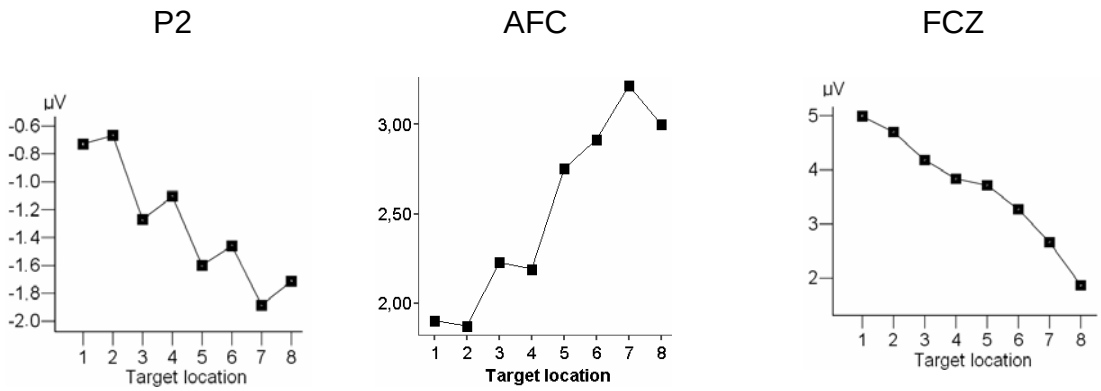

Figure 3-22. Mean amplitude of distance conditions at P2, AFC and FCZ in the time windows 150-200ms (for P2 and AFC) and 250-300ms (for FCZ).

Delay effects

During reproduction the delay manipulation was reflected by significant effects in four of the six time windows (see Table 3-5). In the other two time windows the effects did not reach the significance threshold, but had the same tendency. The F values were broadly distributed, suggesting that differences were narrowly localized at one scalp area (Figure 3-23).
Maximal F-values were found at left parietal electrodes in the 0-50ms time window and near the CZ in the 100-150ms range. The left parietal and anterior frontal F-value distribution of the first time window resembled the topography of the distance effects between 100 and 200 ms. At parietal sites parietal negativity increased with an increase in delay (Post hoc tests at CP3 in the 0-50ms window revealed that all conditions differed significantly from each other (Ps <.05). Over anterior frontal areas, the shortest delay condition showed more negative activity than both others (Ps<.05) at the beginning of the epoch (0-50ms). In the last time-window, in contrast, the most negative amplitudes were found in the longest delay condition (Post hoc tests indicated only a trend towards a more negative amplitude of the longest delay in comparison with both others: “5” vs. “0”, P=.06, “5”vs.”1”, P=.08).

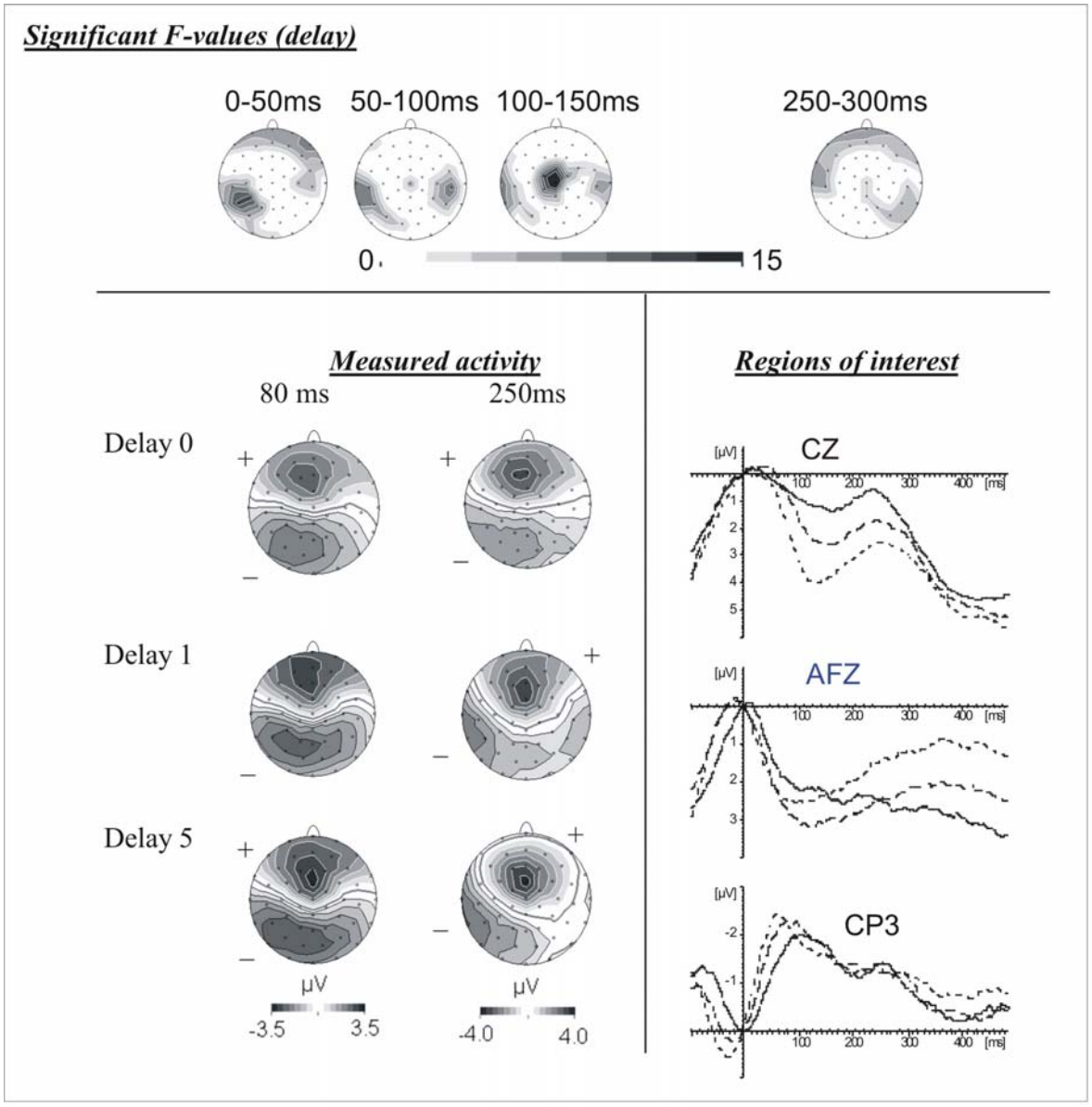

Figure 3-23. *Top*: Significant F values for main effect "delay" as indicated by electrode specific ANOVAs. *Middle left:* topographies of over all distances averaged ERPs for three delay conditions at 80 and 250 ms after the movement onset. *Middle right:* ERPs of delay conditions at Cz, AFZ, CP3 (—— delay "0", - - - delay "1", ... delay "5").

At CZ the maxima of the frontocentral positivity around 150 ms increased with a longer delay period (see Figure 3-23). In the time window 100-150ms all means were significantly different from each other (all Ps <.05).

In addition to the procedures reported so far, we also performed a source analysis. We computed current source density distributions for each data point of the whole time range from the movement onset until the movement endpoint for each of the 24 conditions. These single tomographies were then averaged over the whole epoch, resulting in one mean current density distribution for each experimental condition. Since we were primarily interested in

delay effects, we averaged within each delay condition over the eight distances. The results are shown in Figure 3-24 and Table 3-8.

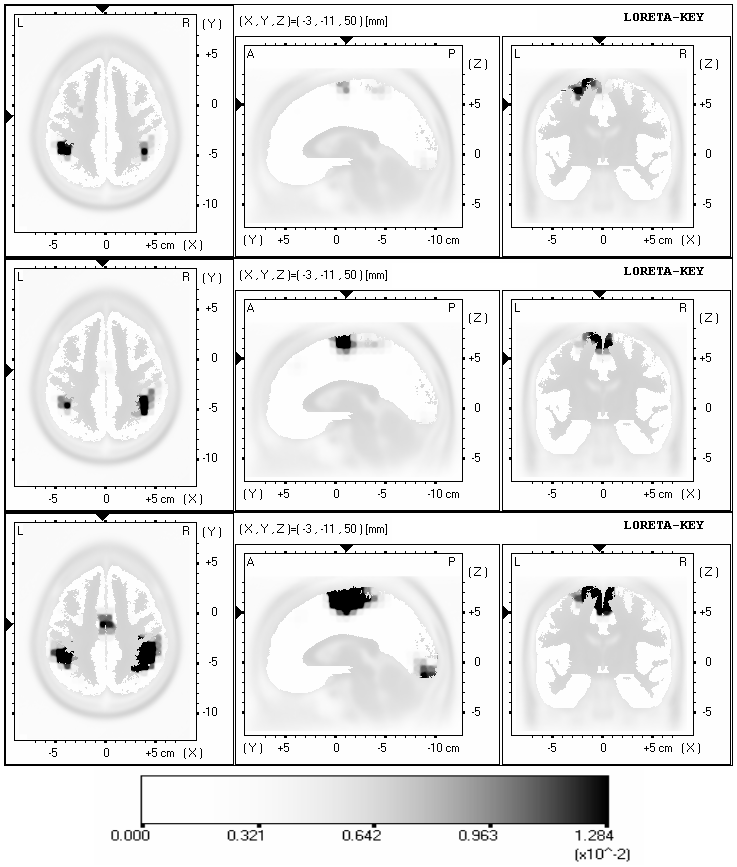

Figure 3-24. LORETA current density distribution in three delay conditions (as indicated by calibration). Activity is color-coded, with maximum corresponding to black and zero to white. Axial, sagittal and coronal slices are here made through a point indicated by X, Y and Z coordinates in Talairach space.

The current density reconstruction in the reproduction phase revealed three main clusters, localized bilateral in the inferior parietal cortex (BA 40) and around the SMA (BA 6). The strength and the exact topography of the activation varied with the delay condition (see Figure 3-24 and Table 3-8). On the one hand, the activity at the precentral sites increased with longer delay. On the other hand, the sensory sources (BA 40) showed a small but clearly detectible drift from left (delay “0”) to right dominant activity (delay “5”). Moreover, in the longest delay condition activity in the parietal areas was stronger than in both other conditions and the “left right asymmetry” was also more pronounced than in the delay “1” and delay “0” conditions. The delay “5” was also associated with a larger number of active clusters in the right hemisphere than both others (“0”: two of seven, “1”: one of five, “5”: seven of ten, see X coordinates in Table 3-8).

In addition, activity within early visual areas was present in all delay conditions.

Table 3-8. LORETA current density of local maxima with activity extended 1x10^-2 (µA).

Delay condition	Anatomical area	Brodmann Area	Talairach coordinates X	Y	Z	Current density (µAx10^-2)
	Inferior parietal lobule	40	-38	-46	50	1.43
	Medial Frontal Gyrus	6	-24	-4	57	1.42
	Superior Frontal Gyrus	6	-17	-11	71	1.34
"0"	Inferior Parietal Lobule	40	39	-46	50	1.31
	Superior Frontal Gyrus	6	25	3	57	1.30
	Inferior Occipital Gyrus	17	-10	-95	-13	1.09
	Paracentral Lobule	4	-3	-39	64	1.02
	Medial Frontal Gyrus	6	-3	-11	64	1.52
	Inferior Parietal Lobule	40	39	-46	50	1.52
"1"	Inferior Parietal Lobule	40	-38	-46	50	1.30
	Paracentral Lobule	4	-3	-39	64	1.07
	Inferior Occipital Gyrus	17	-10	-95	-13	1.05
	Medial Frontal Gyrus	6	-3	-11	64	2.34
	Inferior Parietal Lobule	40	39	-46	50	1.94
	Middle Temporal Gyrus	37	53	-60	-13	1.73
	Inferior Parietal Lobule	40	-38	-46	50	1.61
	Inferior Occipital Gyrus	17	-10	-95	-13	1.61
"5"	Postcentral Gyrus	5	18	-46	71	1.14
	Medial Frontal Gyrus	6	25	-4	57	1.14
	Superior Temporal Gyrus	39	53	-60	22	1.06
	Middle Temporal Gyrus	19	39	-81	22	1.03
	Inferior Occipital Gyrus	18	32	-88	-13	1.03

Discussion

The ERPs during reproduction were comparable to those of the locating phase, although the activity over parietal regions showed a somewhat different time course. While during the first movement a gradually longer lasting negativity was associated with an increase in distance, a phasic wave dominated in the reproduction phase with a greater peak amplitude with increasing distance. This difference may reflect the fact that movements were preplanned according to a common position during encoding (see discussion of the behavioral data), while planning should be very distance specific before reproduction. Thus, the latency differences of the distance conditions obtained in the encoding phase occurred probably as a result of movement- and consequently of process interruption. In contrast, the amplitude modulation during reproduction phase may be due to a distance specific processing characteristic represented by posterior activity. Both results suggest that posterior regions play an important role during movement execution, which may be associated with internal and sensory feedback mechanisms (see also general discussion).

Moreover, the negative peak at frontocentral sites was differently related to the movement time in both phases. The movement time and the peak latency corresponded closely at the near target locations, diverged successively after the fourth target during the location movement, indicating that the negative peak at FCZ preceded the movement endpoint. This comparable negativity during reproduction peaked much earlier and preceded the end of the

movement for about 130 ms in all distance conditions. These results suggest that the process represented by the frontocentral activity starts at about 150ms after the movement onset and reached its maximum at about 120 ms before the movement endpoint. The amplitude and latency are modulated by the distance. We labeled this deflection as N4 according to the literature. The topography of the distance effects, associated with component as well as the according PCA solution were comparable with those obtained during the encoding phase. Since the neuronal origin seems to be in rather precentral regions locating closely to primary motor areas, we assumed that the possible function may be related to executive aspects rather than to a sensory feedback, as previously proposed (Brunia, 1987, see also general discussion).

Additionally, anterior frontal regions were also affected by the distance manipulation. An increase in distance was associated with a decrease in negativity at these sites, especially between 100 and 200 ms after movement onset. We could not identify comparable results and can only speculate that some monitoring processes may be reflected by this activity.

The delay manipulation caused topographical differences during the reproduction phase, which had a broad distribution. These significant topographical changes indicate that the length of the delay interval affects the neural networks activated during reproduction.

The largest delay effects were found around the CZ electrode and seem to arise from a delay specific modulation of P2 (first positive deflection following pre-onset negativities, see Brunia, 1987). It was suggested that this component reflects a central feedback from corollary activity (Arezzo & Vaughan, 1980). According to this, our result would indicate that such central feedback processes may be affected by the delay duration and may be associated with different control strategies detected by the behavior analyses (see also next section (additional analyses)). On the other hand, the P2 modulation was accompanied by a decrease in duration of negative activity with longer delay observed at centroparietal sites in a similar time range (see Figure 3-34 in section “general discussion”) suggesting an increasing involvement of the subjacent areas in information processing with a decrease in delay. Thus, the obvious P2 modulation may also be a result of overlapping with a negative centroparietal component.

Considered as a whole, the delay effects were broadly distributed and allowed only restricted conclusions about essential delay differences. In order to delineate the possible generators we performed a source analysis additionally. By using PCAs we could identify two main sources of variance during the reproduction as well as during the locating movements, suggesting a relatively restricted number of neural generators, which can be expected in parietal and motor areas according to the PCA topographies. The sources identified by LORETA seem to fit the

PCA results. The main current density clusters were found in premotor and motor areas around the SMA and in inferior parietal cortex. Activation of these areas is also reported in a PET study of Darling et al. (2006), who used a comparable kinesthetic matching task[15]. The posterior negative activity peaking early during reproduction (and according distance and delay effects) seems to be related to the sources within inferior parietal cortex (e.g. an increase in current density strength with delay seems to confirm the obtained increase of negative ERPs at posterior locations). Moreover, similarly to the delay phase LORETA solutions suggested a hemispheric shift from left to right with an increase in delay. However, this effect was primarily evident in posterior areas, indicating possible hemispherical differences relating sensory / internal feedback processes. The N4 component appears to be generated in SMA (BA 6) and adjusted areas (primary motor cortex among others). It is worth mentioning that we obtained activity in early visual areas during reproduction, which was also reported by Darling et al. (2006).

3.3.2.7 Additional analyses

By analyzing ERPs of the motor memory task we followed a data driven approach as described in the method section. Initially, we identified “time windows” of interest, which proved to reflect the distance and / or delay manipulations. In subsequent “electrode specific” analyses several electrode locations proved to be affected by the two experimental factors. In order to accentuate the most important effects, PCAs (Principal Component Analyses) and source localization algorithms were used. Such an approach seems to be justified as there are no comparable results available in the literature, although there are also some limitations. For instance, we identified differences in the scaling of maximal acceleration across the eight distances between the delay conditions. Maximal acceleration is assumed to be an early kinematic marker that is almost completely preprogrammed (e.g. Gordon & Ghez, 1987a,b, Messier & Kalaska, 1999). With stimulus-locked ERPs it might be difficult to delineate, corresponding differences in the brain activity preceding movement because of latency jitter of the movement-related brain potentials. In this section we will describe some additional analyses, which aim to provide more detailed information about the electrophysiological markers of the task-specific processes preceding and accompanying the reproduction movement.

[15] In contrast to the current experiment, the hand was displaced by the experimenter during encoding phase in the study of Darling et al.

By analyzing the ERPs around the onset of the reproduction movements we did not detect significant distance differences (see sections 3.3.2.1 and 3.3.2.5). In these analyses we had considered stimulus locked ERPs (synchronized to the second imperative GO-signal). If, however, the onset of the reproduction movement is used as trigger and a late part of the ERPs preceding the onset is analyzed (~ 100ms), delay specific distance differences do become evident over sensorimotor areas, as shown in Figure 3-25.

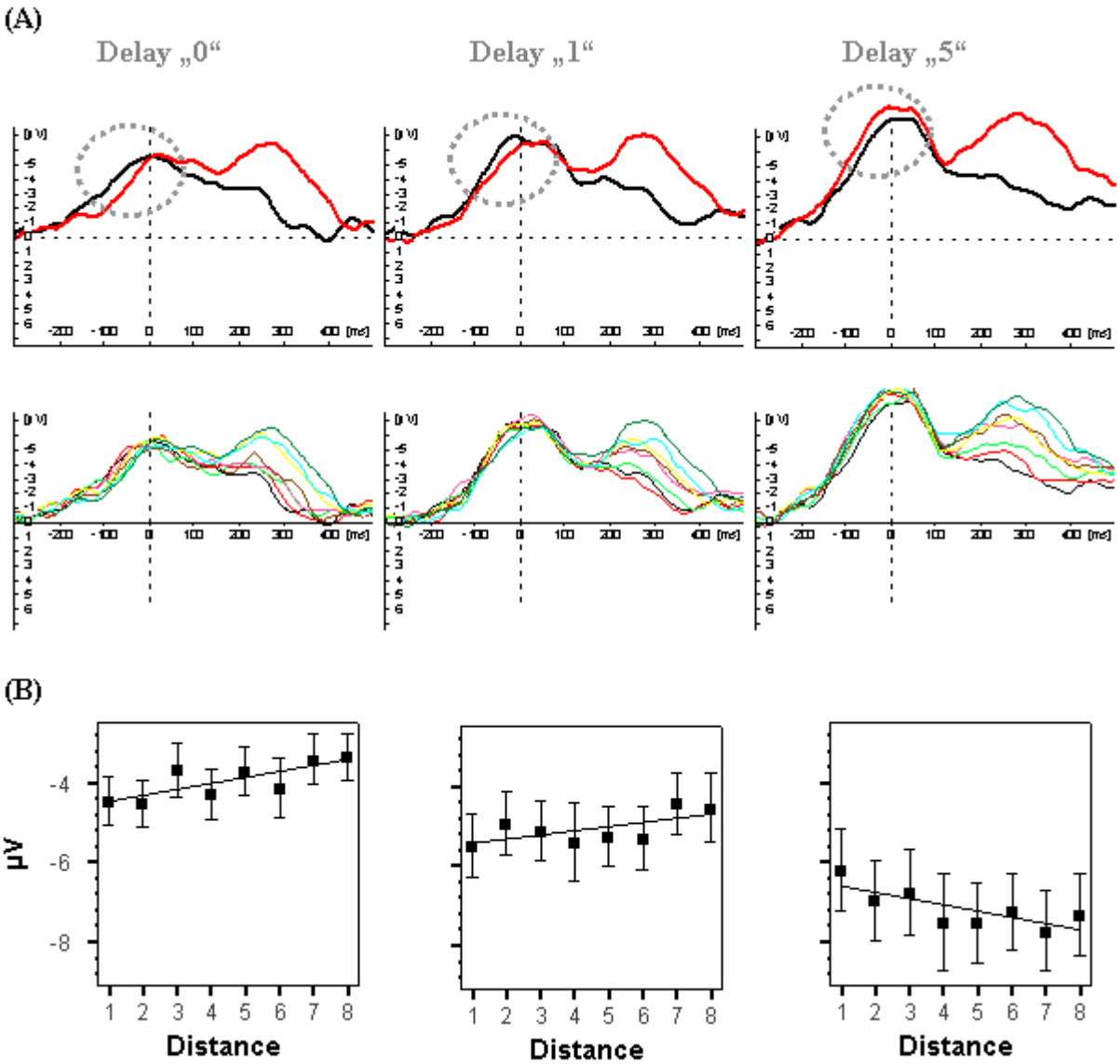

Figure 3-25. (A) ERPs, which were measured at CZ and synchronized to the onset of the reproduction movement (vertical dashed line). *Top:* potential changes of the shortest (black) and the longest (red) distance conditions after the three delays. *Bottom:* ERPs of all eight distances under three delay conditions (different colors reflect eight distance conditions in ascending order: ■ ■ ■ ■ ■ ■ ■ ■ for 1,2,3,4,5,6,7,8). Note: ERPs were adjusted to a baseline of –400 to –300ms. (B) Mean ERP-amplitude in the time window of –100 to –10 ms in respect to the onset of the movement according to the 24 experimental conditions.

The mean amplitude of the ERPs at CZ associated with the preparation of the reproduction after a short delay (“0”) decreased with movement distance. In contrast, with a long delay

(“5”) the ERP amplitude preceding movement onset increased. The evoked activity of the middle delay condition (“1”) was by-and-large unaffected by the distance manipulation. We computed a two-way ANOVA with the within subjects factors “delay” (3 levels) and “distance” (8 levels) on the mean ERP-amplitude at CZ in the time-window between –100 and –10 ms before movement onset. For this analysis, all ERPs were baseline corrected according to the –400 –300ms interval (i.e. the baseline interval lay around the occurrence of the Go-signal). The results of this analysis are shown in Table 3-9 (see row “-100-10ms”). A “delay x distance” interaction became significant indicating delay dependent changes of the ERP amplitude associated with the eight target conditions. When the delay conditions were considered separately, the main effect “distance” reached the significance threshold only in the shortest delay condition (see Table 3-9). However, a trend was also observable in the delay “5” condition (P = .089, see Table 3-9). Moreover, the difference between two extreme distances was significant in the long (P = .042) and in the short (P = .004), but not in the middle delay condition (P = .088).

Furthermore, by analyzing the kinematic parameters of the reproduction phase we obtained that despite the lack of scaling of peak acceleration during reproduction after the shortest delay (“0”), peak velocity and end positions showed systematic distance specific characteristics. We attributed this effect to the “pulse-width” modulation, which allows reaching higher velocities and further positions through the prolongation of an underlying control signal (see discussion of the behavioral data). If this assumption is correct, one would also expect distance differences during an early part of reproduction, especially in the shortest delay condition. By including all electrode locations in the previous analyses, we did not find significant distance effects until 100ms after the movement onset (see Table 3-5). However, considering the ERPs over primary sensorimotor regions, some indices for the assumed processes seem to be present. Figure 3-26 shows the same ERPs as Figure 3-25, from which the activity from –10 to 0 ms in respect to the movement onset was subtracted in order to emphasize possible differences emerging during movement execution (i.e. the same baseline was used as in the previous analyses, for arguments see the method section).

The evoked activity in the early part of reproduction (until ~ 100ms) was characterized by a decline in negative potential preceding the movement onset (MP) in all delay conditions (a similar positive deflection is also labeled as P2, see Brunia, 1987). A precise data inspection revealed that this activity decrease occurred in a distance specific manner, when the delay was short (0): an increase in distance was associated with an obvious approximately linear prolongation of the “decay” of the mentioned deflection. No such relation was evident under

the two other delay conditions. We tested this effect with an ANOVA performed on the mean amplitude in the time window between 0 and 120 ms after the movement onset ("delay" and "distance" served as within subjects factors). As shown in Table 3-9 (row "0-120ms"), the "delay x distance" interaction did not reach the significance threshold. However, a trend was evident, as indicated by a P value of .098. Additionally, when the three delay conditions were separately analyzed, a linear contrast was significant only in the delay "0" condition (P = .022, delay "1": P = .119, delay "5": P = .541). Furthermore, when the two extreme distance conditions ("1" and "8") were compared, they differed significantly from each other only in the shortest delay condition again (see Table 3-9, rows "delay "0": 1vs8", "delay "1": 1vs8" and "delay "5": 1vs8").

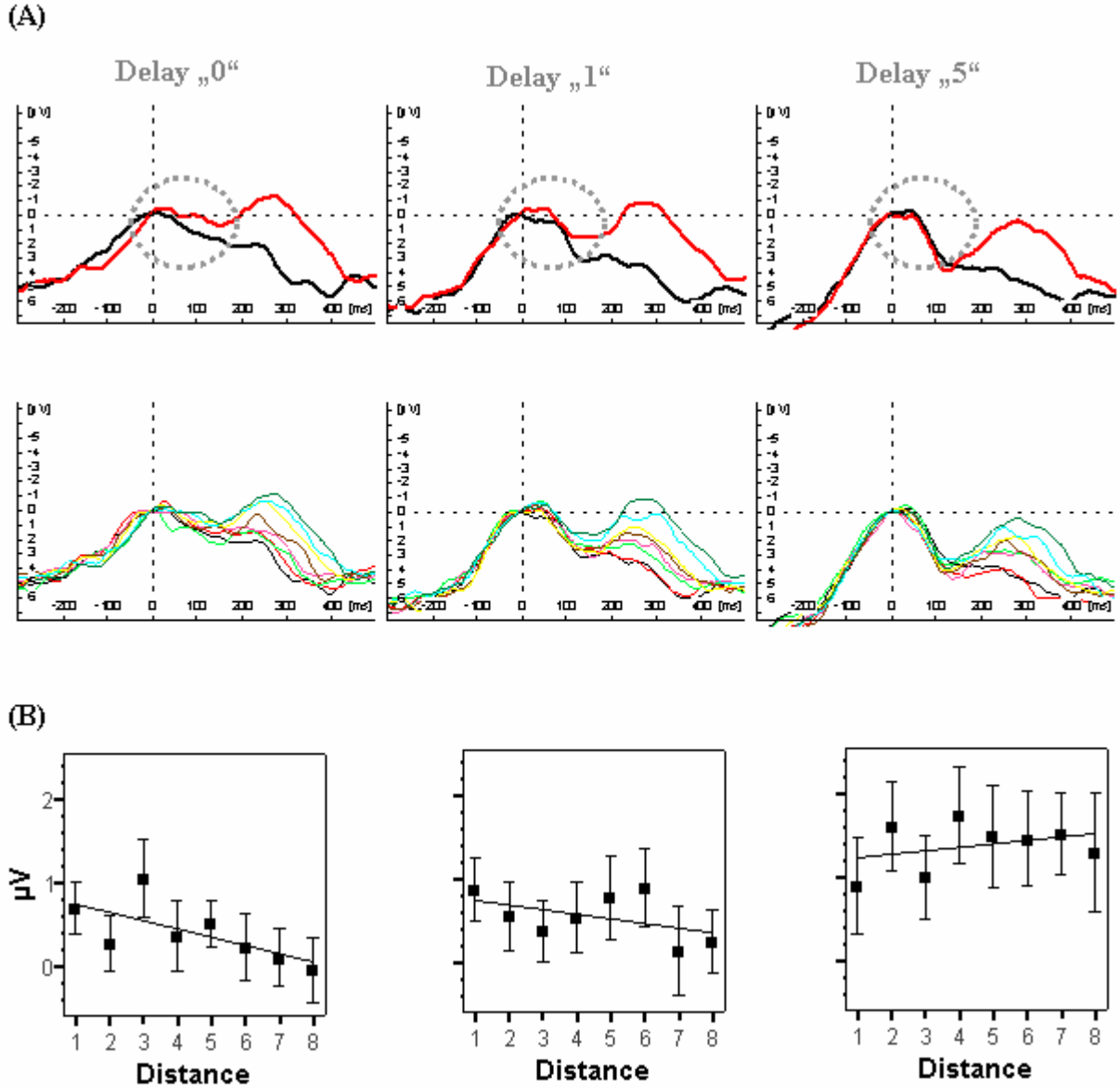

Figure 3-26. (A) ERPs at CZ, which were synchronized to the onset of the reproduction movement (vertical dashed line). *Top:* evoked activity associated with movements to the nearest (black) and to the furthest (red) targets dependent on delay. *Bottom:* ERPs of all eight distances under three delay conditions (different colors reflect eight distances: ■ ■ ■ ■ ■ ■ ■ ■ for 1,2,3,4,5,6,7,8). Note: ERPs were adjusted to a baseline of

–10 to 0ms. (B) Mean ERP-amplitude in the time window of 0 to 120 ms in respect to the onset of the movement according to the 24 experimental conditions.

Table 3-9. Results of statistical analyses preformed with mean amplitude of ERPs at CZ in selected time-windows (see text). Degrees of freedom were corrected according to Huynh and Feldt (1976), when sphericity assumption was violated.

	"delay"			"distance"			"delay x distance"		
	df	F	P	df	F	P	df	F	P
-100-10ms	2,34	**14.90****	**<.001**	7,119	1.63	.132	14,238	**2.33***	**.013**
delay "0"	---	---	---	7,119	**3.60****	**.002**	---	---	---
delay "1"	---	---	---	7,119	1.61	.140	---	---	---
delay "5"	---	---	---	7,119	1.82	.089	---	---	---
0-120ms	2,34	**5.56***	**.019**	7,119	.94	.478	14,238	1.54	.098
delay "0": 1vs8	---	---	---	1,17	**4.55***	**.048**	---	---	---
delay "1": 1vs8	---	---	---	1,17	2.85	.110	---	---	---
delay "5": 1vs8	---	---	---	1,17	.67	.425	---	---	---

Discussion

The motor command for an upcoming movement is assumed to be associated with negative deflections over sensorimotor areas preceding movement onset (Brunia, 1987). The final negative shift is often called "motor potential" (MP or N2, see e.g. Brinia, 1987) and was shown to be affected by manipulations of kinetic and kinematic parameters. An increase in inertial load applied to finger movements led to an increase of the ERP-amplitude in the range between –100 and 0 before movement onset (Slobounov, Tutwiler, Rearick, & Challis, 1999). Kristeva, Cheyne, Lang, Lindinger, and Deecke (1990) reported similar results. A gradual increase in amplitude with an increase in range of motion was also observed previously in the same time range (Slobounov, Rearick, & Chiang, 2000). Moreover, the amplitude of the cortical potentials preceding the response proved to be sensitive to the variation of other variables like movement speed (Cooper & McCallum, 1989) or the rate of force development (Slobounov, Ray, & Simon, 1998).

In the present analysis we observed that the amplitude of the MP component varied as a function of the delay and the distance manipulations. When the delay was short ("0"), the mean amplitude decreased with movement distance. However, at the time of the movement onset, the amplitudes of all distance conditions were comparable (see Figure 3-25). In contrast, a trend towards an increase in ERP-amplitude with distance was observed, when the delay interval was long ("5"). As mentioned, we found differences in the scaling of peak acceleration across the three delay conditions, which were expressed in an increase of differentiation of maximal acceleration values across eight movement distances with an

increase in delay (see behavioral results). Since these differences occurred very early during movement execution (~20ms after the defined movement onset), it seems to be appropriate to relate them to the current ERP results.

The modulation of the initial acceleration (and / or of the AG1 burst visible in EMG) is supposed to result from the variation of a control signal, labeled “force pulse” or “excitation pulse”, whose “height” and “width” can be adjusted to various task situations (see discussion of the behavioral data). Such a pulse has been defined as descending presynaptic input, which converges and summates in the alpha motor neuron pool (Gottlieb et al.1989, Gottlieb, 1993). The spatial and temporal summation of all converging action potentials was assumed to be related to the “pulse height”, while duration of that firing burst was attributed to the “pulse width”.

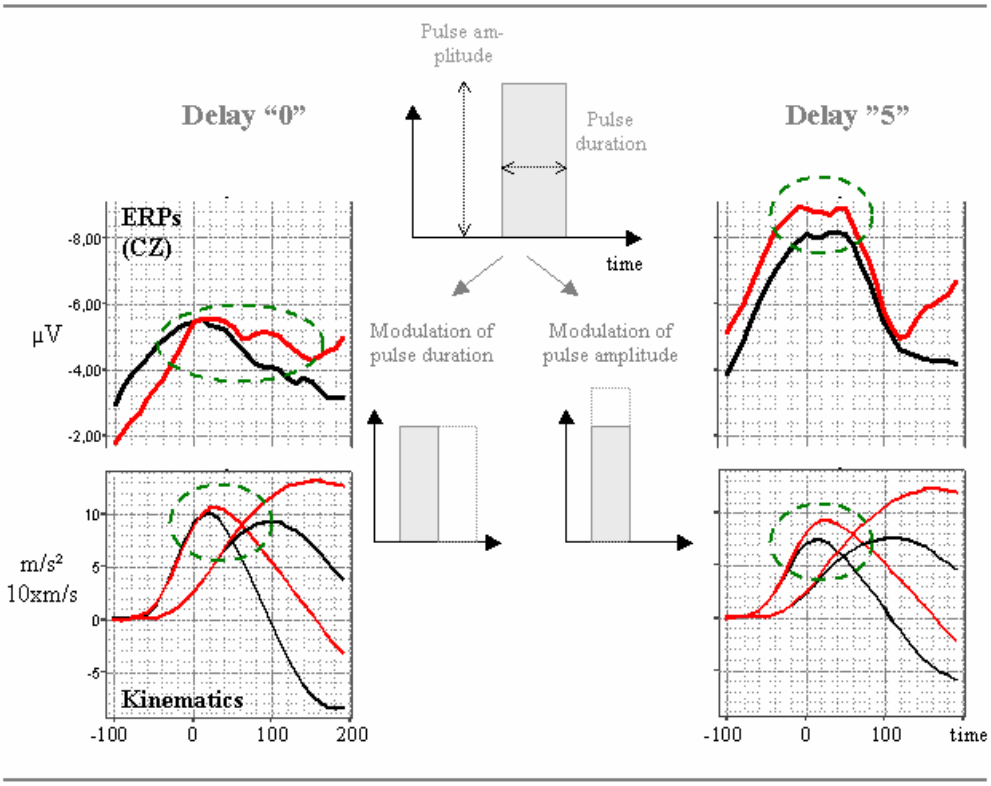

Figure 3-27. The relation between ERPs measured at CZ (time range between –400 and –300 ms before movement onset served as baseline) and acceleration and velocity trajectories shortly before and during reproduction movements to the nearest (black) and the furthest (red) target locations in the two delay conditions (“0” and “5”). The middle part of the Figure shows an assumed mechanism that may be associated with the kinematic and ERP effects. According to this, the modulation of the MP amplitude at the beginning of movement reflects a modulation of the initial intensity of a force pulse by providing an excitatory input to the alpha motor neurons. The detected increase in peak velocity with target distance in the short delay condition is mainly achieved by a longer duration of this excitation with target distance (visible in a longer lasting negativity). In contrasts, an amplitude increase of MP with an increase in movement distance before movement onset in the long delay condition primarily indicates an amplitude modulation of the initial excitation pulse. Note: to emphasize the delay differences, delay specific changes were shown as “pure” duration modulation and as “pure” amplitude modulation mechanisms.

Since the late part of the MRPs ("movement related potentials") can be related to the corticospinal outflow initiating the movement (Kornhuber & Deecke, 1965, Arezzo & Vaughan, 1980, Brunia, 1987), the modulation of its intensity and duration is possibly related to a modulation of the "pulse-high" and "pulse-width" of the initial force pulse. Accordingly, with the shortest delay the amplitude before movement initiation should not vary, but the duration of the negativity during an early phase of the reproduction should increase with increasing distance. In contrast, in the long delay condition, an increase in the MP-amplitude with target distance should occur. Although the effects were rather weak, they are in agreement with the idea that the kinematics of the force pulse, as derived from behavior and EMG, is reflected in the ERPs. Figure 3-27 illustrates the relation between the kinematic and the electrophysiological data before and during reproduction movements to the two extreme target positions ("1" and "8") after two delays ("0" and "5"), as well as the assumed processes underlying the observed effects.

Control of a late part of trajectory

Our previous analysis of the acceleration profiles during the reproduction phase revealed delay dependent and distance specific scaling of peak deceleration, suggesting differences in the control of a late part of the movements across the delay conditions. The ERP results of the reproduction phase, on the other hand, indicated that "distance" and "delay" affected the evoked activity independent from each other, since no significant interactions between "delay" and "distance" and / or "delay", "distance" and "electrode" factors were found. Moreover, the detected "delay" effects were broadly distributed and allowed only restricted statements about possible functional and / or electrophysiological differences.
There may be several reasons for these findings. The delay differences may be rather weak (e.g. they may be present at only few electrode locations) and hence could not be detected by including all recording sites in the superordinate statistical analyses ("time-window specific"). In addition, due to the different movement durations the late phase of the reproduction epoch was not fully comparable across experimental conditions (e.g.: A movement to a near target has a shorter duration than a movement to a far target. Thus, the EEG prevailing during the "late" part of a short movement was compared with the EEG prevailing during a "middle" part of a longer movement). Furthermore, if there are processes, which are coupled with the end-position of a movement rather than with its onset, they would also not be adequately detected by the previous analysis.

Therefore, in the analysis to be described here we used the end position as trigger and focused on the "late" range of movement reproduction (the last 200ms before end position). The evoked activity in the first 100 ms after the end point served as baseline. This type of baseline correction appeared to be appropriate, since we did not expect processing differences after movement execution. We analyzed the three delay conditions separately in order to be able to also detect weak effects, which may be associated with the kinematic differences mentioned above.

Figure 3-28 shows the evoked activity during the reproduction phase of all 24 experimental conditions at electrodes located closely to the sensorimotor regions. The ERPs synchronized to movement onset and baseline corrected according to the interval of -10 to 0 ms are shown in the left part of the Figure (this activity entered the previous analysis). The evoked activity including the same trials, but synchronized to the movement end position and baseline corrected, as mentioned above, is shown on the right side.

The largest distance differences identified by the prior procedure were localized at frontocentral to centroparietal electrode locations and were found in the last chosen time window (250-300ms in respect to the movement onset, see 3.3.2.6). Moreover, the highest F-values were found at left hemispheric sites, what is also confirmed by the visual data inspection. As shown in Figure 3-28 (right), such a laterality effect vanishes, when end position-locked activity is considered.

Figure 3-29 illustrates the F-score distribution of the significant main effect "distance", which were computed for each delay condition and each electrode separately in the time windows -200-100 ms and -100-0 ms before the end position. The main clusters of significant distance effects are located at centroparietal to frontocentral sites. However, delay differences also became evident. The F-scores of the shortest delay condition clustered around postcentral locations and frontocental differences had left hemispheric bias in the last time window. In contrast, the longest delay condition was associated with distance effects localized more over the right hemisphere and weaker effects over posterior regions.

The current source density (CSD) maps of the last 200 ms before end position are shown in Figure 3-30. These topographies correspond quite well with the statistical maps shown in Figure 3-29. Especially, the laterality bias in the longest delay condition resembles the F-value distributions of both time windows.

Based on these observations, we performed a laterality analysis including four electrodes: FC1, FC2, CP1, CP2. Figure 3-31 shows the corresponding ERPs, which were averaged over all distance conditions.

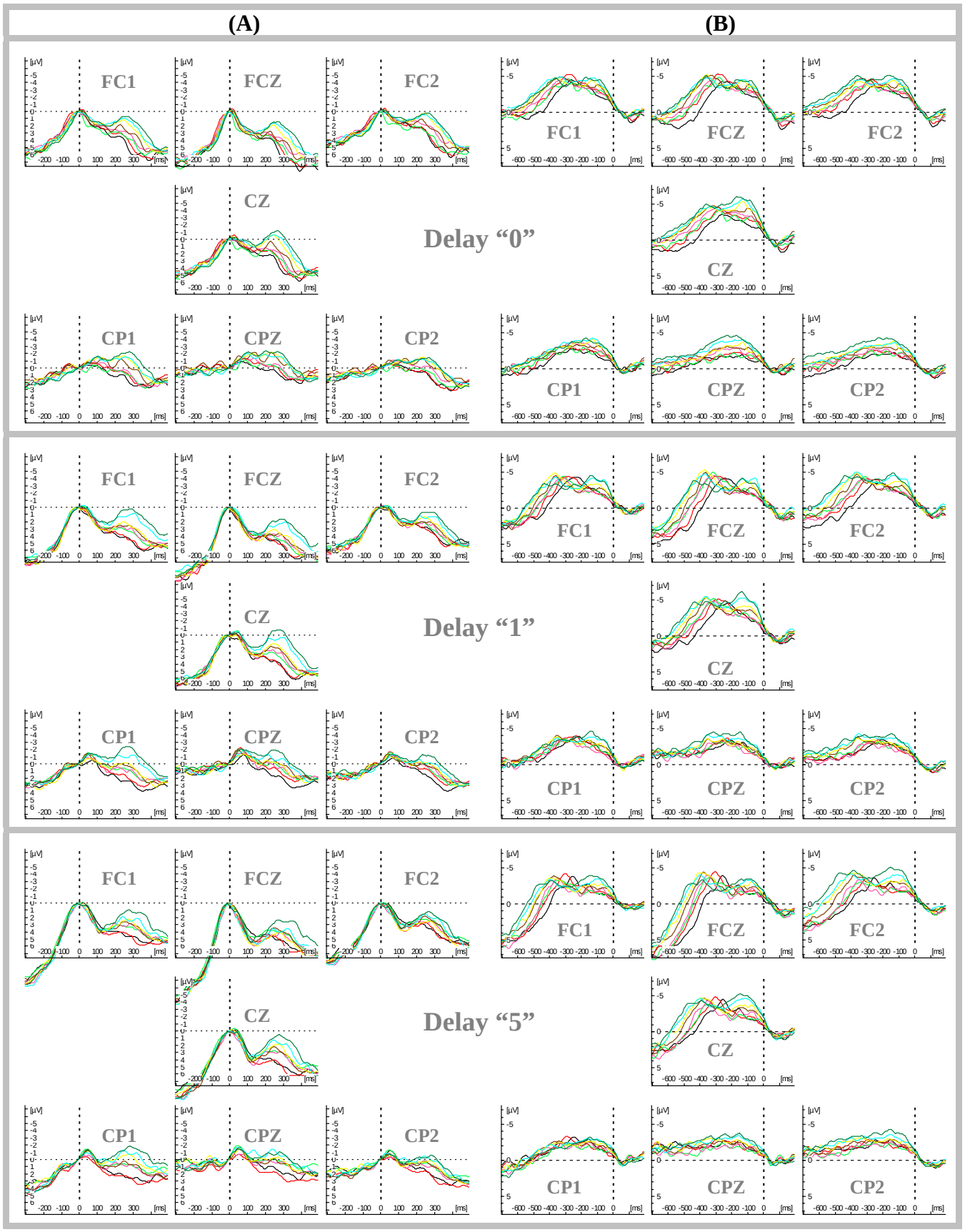

Figure 3-28. ERPs of the reproduction phase at selected electrode locations adjusted to the movement onset (A) and to the movement endpoint (B). Baselines were determined as the mean activity in the interval between –10 and 0ms for (A) and between 0 and 100ms for (B). Note: all ERPs were low-pass filtered (20Hz) and different colors reflect eight distances: ■ ■ ■ ■ ■ ■ ■ ■ for 1,2,3,4,5,6,7,8.

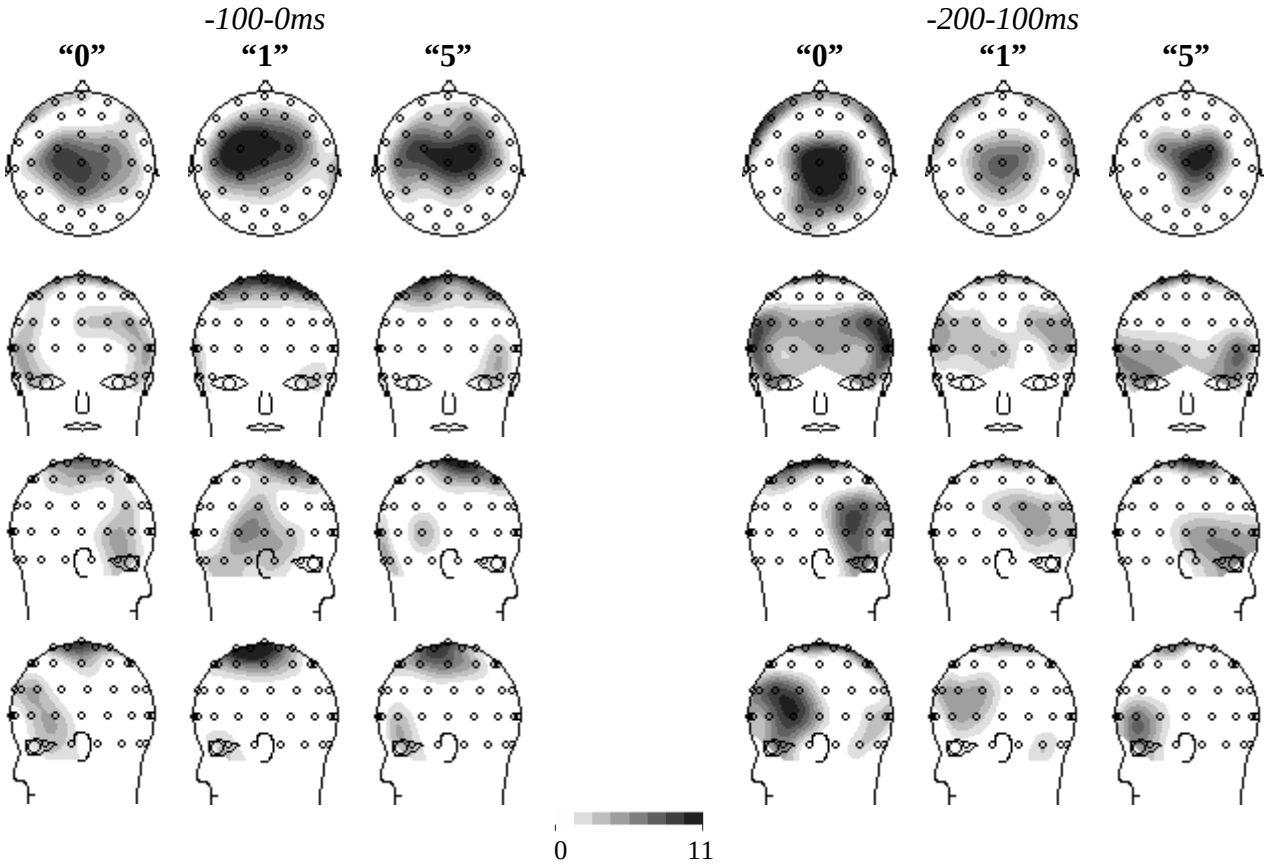

Figure 3-29. Topographical maps of F-values for factor “distance” computed for each delay condition separately (labeled as “0”, “1” and “5”) in two selected time windows (-200-100 and –100-0ms in respect to the movement endpoint). For descriptive purpose an interpolation by spherical splines was used.

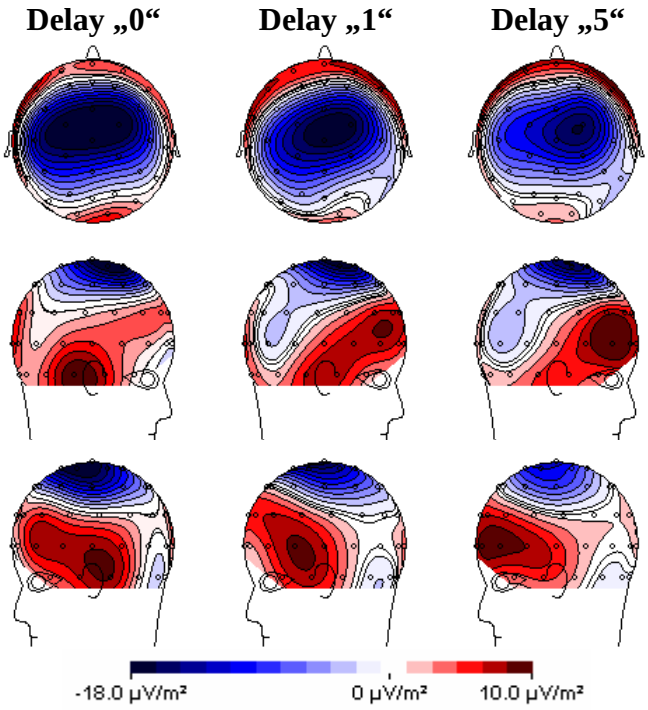

Figure 3-30. Current Source Density (CSD) computed for the 200 ms before end position and averaged over eight distance conditions according to the three delays. Note: a spherical interpolation was used and an interval of 0-100ms after the endpoint served as baseline.

In the longest delay condition, the ERPs had a higher amplitude over the right hemisphere, as already disclosed by the F-value and CSD topographies. In the shortest delay condition the trend was reversed. Table 3-10 summarizes the ANOVA results, with repeated measures factors “laterality” (left vs. right), “anteriority” (postcentral vs. precentral), “delay” (“0”,”1”,”5”) and “distance” (8 distances). The question of interest was whether factor delay interacted with factor laterality. As shown in Table 3-10, this seems to be the case. The mean amplitude values averaged over the corresponding pair of electrodes of each hemisphere and all distance conditions are shown in Figure 3-32.

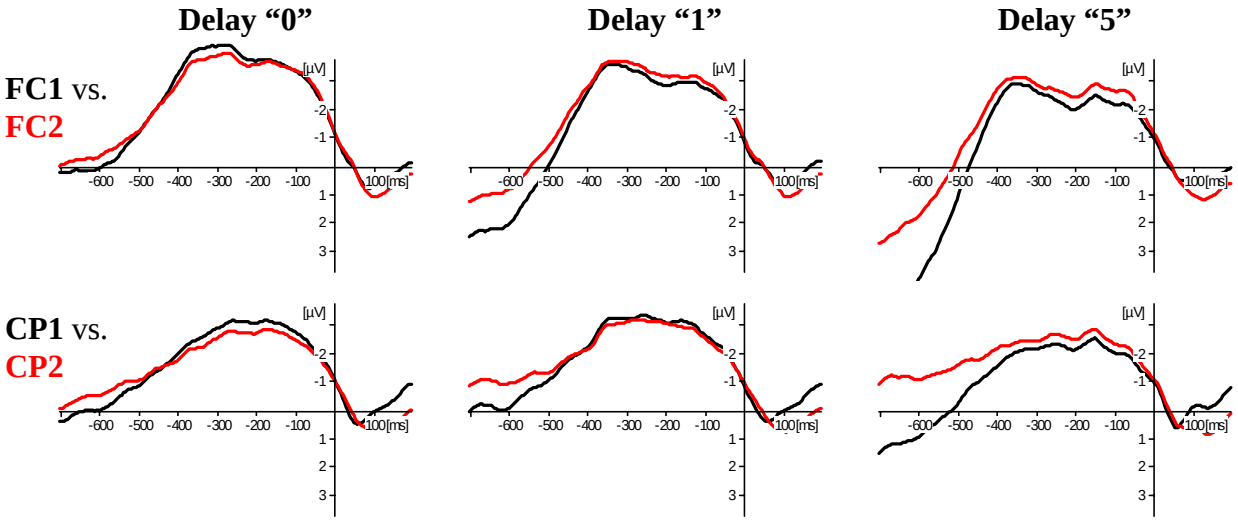

Figure 3-31. ERPs of the reproduction phase at FC1 (black), FC2 (red), CP1 (black) and CP2 (red) in three delay conditions. The time scale is adjusted to the latency of movement end position (t=0). The interval between 0 and 100ms was used for baseline correction.

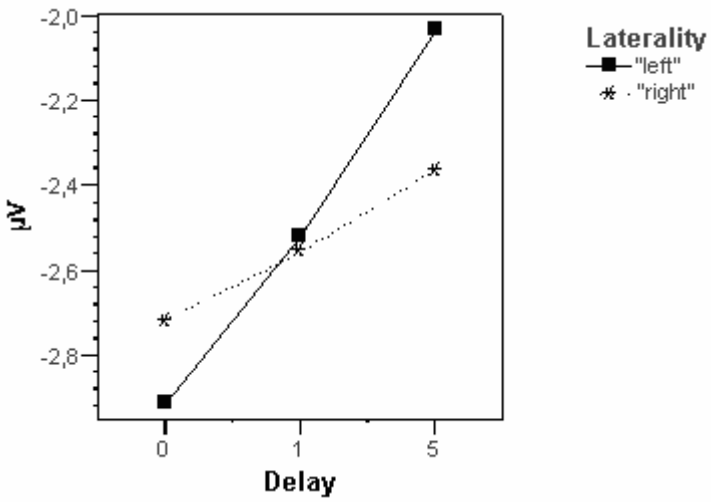

Figure 3-32. Mean voltage amplitude measured at FC1 and CP1 (“left”) and at FC2 and CP2 (“right”) in the three delay conditions.

This analysis suggests that movement control during a late phase of execution was associated with stronger activity of sensorimotor areas contralateral to the moving hand when the delay

was short (“0”) and with an ipsilateral dominance when the delay was long (“5”). The middle delay condition showed no systematic laterality effects.

Table 3-10. Results of a “laterality analysis”. Degrees of freedom were corrected according to Huynh and Feldt (1976). For further details see text.

Effect	df	F	P
“laterality”	1,17	.20	.661
“anteriority”	1,17	2.02	.174
“delay”	2,34	**6.71****	**.003**
“distance”	7,119	**20.10****	**<.001**
“laterality & anteriority”	1,17	1.42	.250
“laterality & delay”	2,34	**4.09***	**.032**
“anteriority & delay”	2,34	**9.75****	**.002**
“laterality & anteriority & delay”	2,34	.30	.615
“laterality & distance”	7,119	1.11	.359
“anteriority & distance”	7,119	1.41	.250
“laterality & anteriority & distance”	7,119	1.02	.362
“delay & distance”	14,238	.89	.561
“laterality & delay & distance”	14,238	1.69	.117
“anteriority & delay & distance”	14,238	**2.30***	**.033**
“laterality & anteriority & delay & distance”	14,238	.88	.442

Discussion

The largest distance effects were obtained over primary sensorimotor areas in the stimulus-locked as well as in the response-locked analyses. These were mainly caused by a distance specific modulation of an ERP component, which we labeled as “N4” according to the literature (e.g. Brunia, 1987). Its topography as well as its possible neuronal origin indicated by a source analysis suggested that this component is generated in regions located closely to the primary motor area.

The current analyses provide some further insights into possible mechanisms, which are dominant at the end of the movements and which may also be related to the N4. The clusters of the detected distance effects as well as the maximal negative activity in a late phase of the movement indicate a stronger involvement of the ipsilateral, right hemisphere, when the delay interval was long. In contrast, when the delay was short the end phase of the reproduction was associated with stronger activity contralateral to the moving hand, i.e. in the left-hemisphere. Moreover, with a long delay stronger distance effects were detected at posterior recording sites. These results may be related to the delay dependent kinematic changes occurring during deceleration.

It has been claimed that there is a hemispherical specialization of motor control ("dynamic dominance hypothesis"), saying that the left hemisphere controls dynamic aspects of movements (e.g. control of limb trajectory), while the right hemisphere regulates static features as limb position and posture (e.g. Sainburg & Schaefer, 2004, for a recent review see Serrien et al., 2006). Our correlation analysis performed with the behavioral data suggested that an increase in delay attenuated dynamic and, simultaneously, amplified static control mechanisms. Accordingly, one may assume that the stronger involvement of the right hemisphere in the long delay condition indicates a stronger emphasis of a static parameter like end posture or end position. The stronger left hemispherical activity during reproduction after the shortest delay, in contrast, may be associated with dynamic control processes.

3.4 General discussion

We studied working memory correlates of linear movements of different length with varying delay intervals between encoding and reproduction. Kinematic profiles and event-related brain potentials were systematically analyzed for distance and delay dependent changes. The acceleration profiles showed that the amplitude of acceleration and deceleration peaks was systematically related to the length of the movement. The amount of the gradual changes with increasing distance, i.e. the distance dependent "scaling" of the peak parameters, proved to be delay dependent. The results suggest that movements in the shortest delay condition relied more on dynamic control mechanisms (e.g. a control of movement duration), while reproduction movements after longer delays were more dependent on a control of static variables (e.g. end point distance).

The ERP analysis yielded condition specific differences of peak amplitudes of various components in distinct processing epochs. In order to reduce the amount of data and to focus on essential processing aspects, we used PCAs and a source analysis procedure. In the following we try to integrate the main results.

Motor programming and on-line control

During rapid arm movements a triphasic EMG pattern is typically observed (for review see e.g. Berardelli et al., 1996). In contrast to slow movements, which are characterized by continuous EMG activity, rapid joint displacements are produced by two phasic contractions of the agonist muscle (labeled AG1 and AG2) at the beginning and at the end of the movement, and an intermediate burst in the antagonist muscle (ANT). The AG1 activation seems to provide the force to start the movement, which is decelerated by the following antagonist activity (ANT). The second phasic agonist activation (AG2) is assumed to terminate the decelerative force pulse and, thus, stabilizes the limb at the end of the movement. MacKinnon and Rothwell (2000) suggested that the AG2 burst may also be related to reafferent feedback mechanisms that adjust the actual to the stored movement representation (see Mills & Kimiskidis, 1996, for similar hypothesis).

There is some evidence that M1 (primary motor cortex) plays a key role in generating phasic muscle activity (Sergio & Kalaska, 1998, Sergio, Hamel-Paquet, & Kalaska, 2005). By measuring neural responses of neurons in caudal primary motor cortex of monkeys, these studies showed that motor signals during reaching do not have a simple, ramp-like characteristic. Rather, the response characteristic of many cells (61%) corresponded to the

muscle activity, as expressed in force profiles and the EMG signal. Therefore, the authors suggest that all components of the triphasic EMG signal are generated in M1.

Within the EEG research the motor command is assumed to be reflected in a negative potential occurring over sensorimotor areas before movement onset (MP). In the present study we observed that this deflection was affected by both delay and distance of the reproduction movement. While delay effects as such proved to be difficult to evaluate, the more specific delay-dependent distance differences shortly before and after movement onset provide some insights into the nature of the later programming stages. Our analyses seem to indicate that the modulation of the MP (i.e. of its amplitude and duration) can be defined as a modulation of the first control signal ("force pulse" or "excitation pulse") that was proposed to describe kinematic and EMG data (see e.g. Gottlieb et al., 1989). Thus, the MP appears to be associated with the acceleration of the limb and accordingly, with the first agonist muscle activity that controls the initial part of movement trajectory (see e.g. Gordon & Ghez, 1984, Ghez & Gordon, 1987, Gordon & Ghez, 1987a, Brown & Cooke, 1990, Cooke & Brown, 1994, Gottlieb et al., 1989 for evidence of a close relation between acceleration and AG1).

While the EPRs preceding movement onset, like RP and MP, are well-established, the knowledge about post-onset deflections is limited. Most of them were attributed to sensory and internal feedback processes. Our PCA analyses of the two movement epochs delineated two components that explained most of the variance and that were modulated by movement length. According to the PCA topographies, we expected two main clusters of sources, one in precentral regions near the primary motor cortex and one in the parietal cortex. Accordingly, LORETA estimates indicated "motor" activity in SMA and adjusted areas as well as bilateral activation of inferior parietal cortex (BA 40) in all delay conditions. However, the time courses of activation over these regions were quite different.

The latency of the second negative peak over frontocentral and central regions corresponded closely with the peak deceleration in all eight target conditions. However, this correspondence has to remain descriptive, because peak latency could not be determined exactly due to a poor quality of EEG data. As mentioned, changes in acceleration are closely related to muscle activity measured by EMG. Thus, the negative ERP component (N4) could be related to the activity in the antagonist muscle (ANT) that decelerates the limb. The present study is to our knowledge the first that reports systematic and distance specific modulations of the N4 component in the movement related ERP. This component seems to play an important role in the control of movement execution.

A negative component over parietal areas peaked shortly after movement onset and before the peak velocity was reached and lasted approximately until the end of the forward movement. The timing of this component suggests that it reflects a process between movement on- and offset that may be related to sensory or / and internal feedback mechanisms.
We also obtained distance effects over frontal regions, which may reflect some monitoring aspects of movement execution.
These results seem to fit rather well into a broad context of motor control processes. According to the classic theory of motor control, reaching movements have two components, an initial ballistic one, which is associated with a rapid motion of the limb and based on a pre-programmed motor plan, and a late adjustment phase at the end of the movement that is dependent on feedback signals (e.g. Desmurget & Grafton, 2000). On the other hand, the two central commands are assumed to become manifest in the muscle activity as a "pulse" and a "step" signal. According to this, our results are compatible with the idea that activity over motor areas (N4) is related to a signal that determines the late phase of the movement by deceleration and / or termination of deceleration (i.e. by controlling of ANT and / or AG2 activity e.g. as a "step command"). In contrast, activity in sensory areas may represent an intermediate stage of processing related to sensory or / and internal feedback mechanisms (see e.g. Oztop, Wolpert, & Kawato, 2005).
Figure 3-33 summarizes the main results from kinematic and ERP analyses and some possible functional aspects discussed so far.

The delay manipulation led to significant changes of ERP amplitude in several time segments of the motor programming and the motor control phase. They were topographically broadly distributed and allowed only restricted conclusions. A characteristic effect in the short delay condition ("0") in both phases was found at centroparietal locations. During both phases more negative activity (and stronger distance effects in the end position-locked ERPs) was present at these locations as compared with both other delay conditions. Moreover, during the late range of the MC phase we obtained a shift of maximal negativity over sensorimotor areas from the left to the right hemisphere with an increase in delay. This result agrees with the already mentioned "dynamic dominance hypothesis" suggesting a different contribution of both hemispheres to the control of movement parameters (e.g. Sainburg & Schaefer, 2004). The left hemisphere is assumed to be associated with dynamic control mechanisms, while the right hemisphere controls more static aspects. In addition, the result also agrees with the

behavioral results, which indicated a shift from more dynamic to more static control of reproduction with an increase in delay.

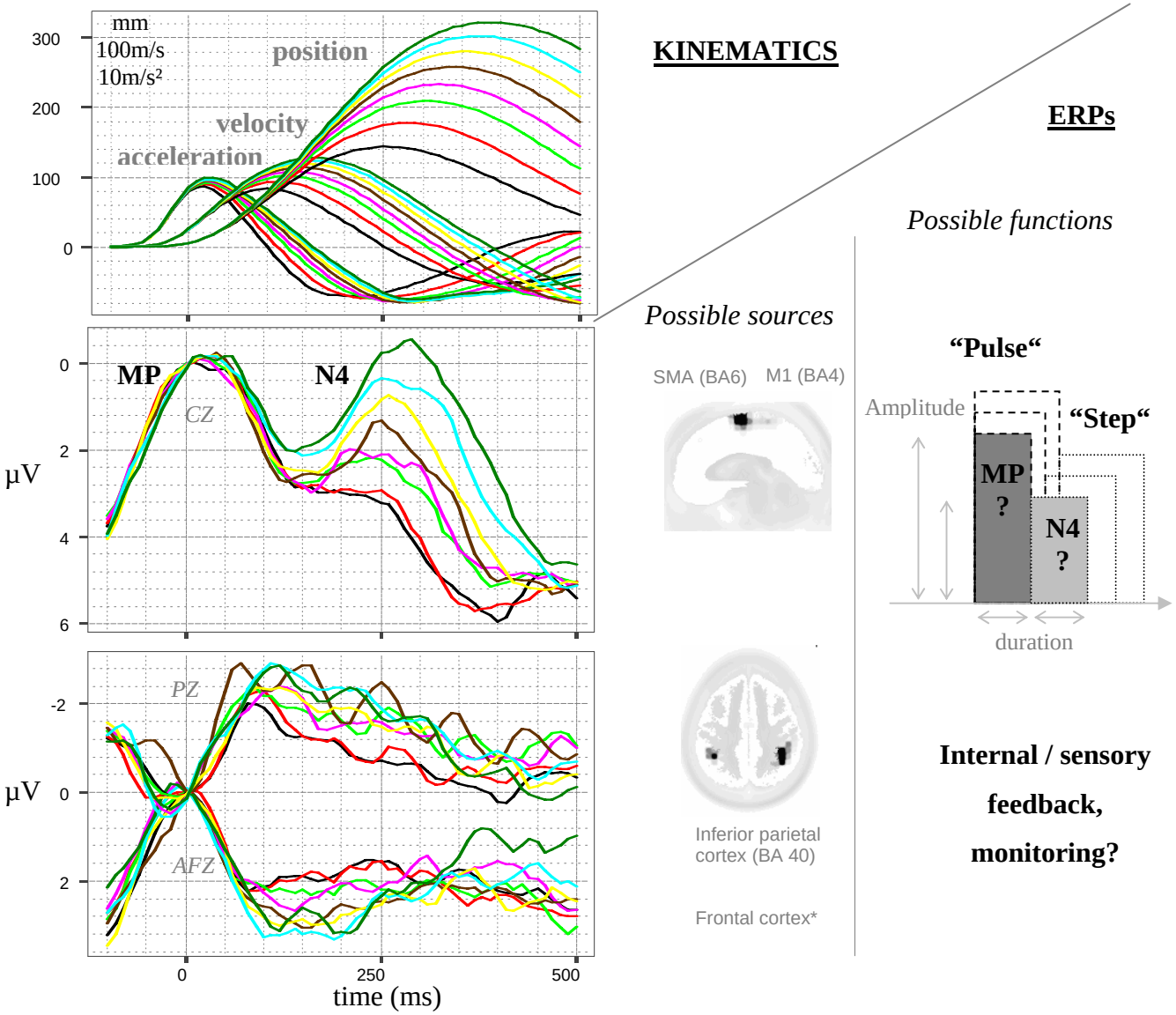

Figure 3-33. *Left*: kinematic profiles and ERPs at CZ, AFZ and PZ during reproduction movements. The time scale is adjusted to the movement onset and ERPs are baseline corrected according to the –10-0ms interval. The color of lines indicates the eight target conditions: ■ ■ ■ ■ ■ ■ ■ ■ = 1,2,3,4,5,6,7,8. *Middle*: locations of main current source density clusters as indicated by the LORETA algorithm for the intermediate delay condition during the reproduction (the results of the two other delay conditions were highly comparable). Despite the distance effects identified at anterior frontal regions, no activity was found in these areas. *Right*: Possible functional aspects associated with the measured evoked activity (see text).

Encoding and retention

In the encoding phase a prominent component appeared at centroparietal electrodes that peaked after the movement had been terminated by the mechanical stop. This centroparietal wave resembled the well-known P300 deflection. The relation of this component to memory

processes, especially to the encoding of information, was extensively studied (see e.g. Rugg, 1995) and its latency is considered to be a good predictor of the timing of stimulus evaluation processes (Coles et al., 1995). A short latency indicates an effective and fast analysis, while longer P300 latencies go together with longer evaluation times and more difficult discriminability. We observed a contingent increase in the latency of a P300 like component with decreasing distance possibly suggesting a gradual increase in categorization difficulty with shorter distances. What may be the reason for this unexpected finding?
It can be assumed that after initiating a movement the "current state" of the system is estimated by continuously updating sensory and motor information (e.g. Wolpert & Ghahramani, 2000, Wolpert, Goodbody, & Husain, 1998). In our task the locating movement was terminated by a mechanical stop at an arbitrary location. It seems likely that all locating movements aimed initially at a far position, as indicated by the behavioral data. Experiencing a mechanical stop soon after movement start will cause a large discrepancy between motor command and sensory feedback. This discrepancy should become smaller with increasing distances, because the experienced stop will be closer to the aimed location. A larger discrepancy will lead to more extensive evaluation processes and this could be the reason why P300 peaks later with shorter movements. This conclusion can also explain the gradual decrease in response variability with an increase in distance. According to this, the evaluation process would affect the memory trace stability and consequently, the reproduction performance. However, we do not know to what extent the observed effect may reflect the modulation of the classical P300. The topography of the related PCA component was restricted mainly to centroparietal locations. The peak latencies were shorter than that reported for the classic P300. Thus, the results should be considered as tentative.
Distance effects were also obtained at frontal sites, at which stronger negativity was obtained for short movements. We assume that they may be related to error detection and correction mechanisms associated with the mentioned conflict.

Processing during retention periods in typical delayed tasks tap working memory functions, primarily consisting of transient storage and manipulation of goal-related information. In the present experiment, the information to be stored concerns positional signals, as posture or derived location, as well as some dynamic and motor program information. A critical question in the present study was whether the CNS stores and uses the same type of information sources for the reproduction movement irrespective of the length of the delay. If processing characteristics are the same in all delay conditions, one would expect highly similar generator

constellations. Our data do not support this notion, because there were substantial topographic differences between the three delay conditions. On the other hand, the temporal dynamics seem to be highly similar, i.e. distinct cortical networks seem to be activated with similar timing characteristics. However, the result should be interpreted with caution. We only found one paper (Lutzenberger et al., 1981), in which the same signal composition was observed during anticipation in a series of 7 CNV studies, using a fixed interval of 6 seconds. Moreover, the PCA methodology has its limitations and the phenomena in short and long delay intervals may have different generators although they can be described with a set of three highly similar factors in each case.

Nevertheless, a decreasing “O-Wave” and an increasing “E-wave” are robust findings in the CNV literature even in short intervals under one second.

Moreover, the firing characteristics of neurons in many posterior sensory and frontal executive areas often show similar properties in working memory tasks, characterized by increasing, decreasing or intermediately peaking activity during the delay interval (e.g. Zipser, Kehoe, Littlewort, & Fuster, 1993, Quintana & Fuster, 1999, Rainer & Miller, 2002). This activity has been associated with diverse memory and planning functions, including target selection, motor preparation, reward, anticipatory stimulus coding etc. According to Fuster (2001), such a pattern, especially with waning and waxing activity, represents two neuronal substrates of an active memory representation with complementary functions. Sensory coupled units (decreasing activity) are assumed to represent a working memory component of perceptual information, while the neuron populations with increasing activity belong to the motor system that primes the anticipated action.

This suggests parallels between EEG and single neuron recordings. The early O-wave observed in CNV paradigms proved to be sensitive to characteristics of the first stimulus, and has been related functionally to an orientation reaction (e.g. Brunia & van Boxtel, 2000). The late “expectancy wave”, in contrast, is thought to reflect motor preparation (Rohrbaugh & Gaillard, 1983), but also can in certain task situations reflect nonmotor characteristics (Brunia & van Boxtel, 2000). Consequently, the amplitude and the scalp distribution of the late wave varies from task to task (Brunia & van Boxtel, 2000, Gevins & Cutillo, 1995, Leuthold, Sommer, & Ulrich, 2004) and has a varying set of source generators (e.g. Cui, Egkher, et al. 2000). These finding are consistent with the sensory-motor mechanism, proposed by Fuster (see above), as well as with a general view of the functional role of slow potential changes (Rösler, et al. 1997), saying that they are associated with the allocation of resources to distinct cortical modules dependent on task requirements and processing stages.

In contrast to the similar temporal aspects of evoked activity, the spatial information derived from topographies and source analysis during the late part of the retention interval suggested different neuronal substrates depending on delay condition. When the retention interval was middle (“1”) or long (“5”) the main activity clusters were found over frontal and parietal regions. Some indices suggest distinct networks within premotor and parietal areas in both delay conditions and different “polarity – location” characteristics of slow waves (i.e. different locations showed positive and negative going slow waves depending on delay) indicate functional differences.

During the shortest delay interval (“0”) the main negative activity was obtained over SMA and left sensorimotor cortex, emphasizing the role of these regions in retention and / or motor preparation.

Similarly to the late phase of movement execution, a pronounced difference across delay conditions consisted in a delay specific laterality of activity at frontocentral locations. Under the shortest delay condition (“0”) a larger negative amplitude was observed over the left than over the right hemisphere. This laterality bias decreased, when an interval of 1 second was introduced and in the delay condition of 5 seconds a higher negative amplitude was present over the right than over the left hemisphere. This result suggests that each hemisphere participates to a different degree in maintaining movement relevant information depending on the delay duration. The laterality differences agree with the mentioned “dynamic dominance hypothesis”, proposed by Sainburg and colleagues, which suggests that the dominant hemisphere system is specialized for controlling limb trajectory, whereas the nondominant system controls limb position or posture (Bagesteiro & Sainburg, 2002, 2003, Sainburg & Kalakanis 2000, Sainburg & Wang, 2002). According to this, activity in the left hemisphere during the late delay phase would reflect a presetting of networks rather than processing dynamic information, while activity localized in the right hemisphere is associated with the preparation of static control parameters. This conclusion seems also to be in line with our behavioral results.

3.5 Summary and conclusions

The primary goal of the present study was to investigate behavioral and EEG effects in a delayed motor memory task. By manipulating the movement distance and the duration of a delay period, we could identify several distance and delay specific changes of behavioral parameters and of ERP measures.

We observed a distance specific biphasic activation over motor areas during movement execution that may reflect two command components previously described by others, i.e. an initial “pulse” and a delayed “step” signal. In addition, we observed an activation of parietal areas between the two motor cortex signals, which is possibly related to internal or sensory feedback mechanisms.

The encoding processes became manifest in a P300 like component over centroparietal areas, whose peak latency increased with decreasing movement length. This result seems to confirm an assumption that the strength of an initial memory trace is defined by an updating of input and output signals.

During the delay period a decreasing, a centrally peaking and an increasing waves were observed that resembled the results obtained with the CNV paradigm and that were also similar to the time courses observed in single neuron recordings in delayed memory tasks.

An important goal of the experiment was to investigate the role of the delay duration on behavior and brain activity. Our behavioral analyses strongly suggest delay dependent changes of the involved control mechanisms being expressed in a transition from a more dynamic (in the shortest delay condition) to a more static control principle (in the longest delay condition). The ERP data indicated different contributions of the two hemispheres to processing with a stronger involvement of the left hemisphere in the shortest delay condition, and a gradual increase in activity in the right hemisphere with longer delays. These results are compatible with the “dynamic dominance hypothesis”, which assumes a left hemispheric control of limb trajectory and a right hemispheric control of limb position and posture.

Our study was mainly exploratory intending to show that combining EEG and kinematic measures can be useful to investigate the details of motor processing. The results indicate that even a “simple” variable as delay duration can cause substantial changes in sensory-motor processing which become manifest in both kinematic and electrophysiological parameters. The changes can be attributed to different sensorimotor modes. In the delay “0” condition with an immediate reproduction the “pragmatic” action-system seems to be dominant, while in conditions with longer delays movement memory seems more dependent on the perception based cognitive processes. The results support the notion that the system exploits several

distinct processes in a highly adaptive manner including different representation levels. These comprise a brief sensory store that represents the dynamics of the first movement, a more permanent representation of the spatial location of the target or hand, and possibly another transient representation of the final body posture. This view is in line with the idea that hierarchical levels exist for perception-action integration (Fuster, 2001, 2004).

4 EEG-Study 2: “Electrophysiological indicators of visuomotor processes: distance specific and delay dependent effects”

4.1 Introduction

In order to make a movement towards a visual target, the CNS has to transform retinal information about target location into an appropriate motor command that specifies patterns of muscle activity of a joint. It was assumed that information about target location and information about the current position of the joint must be integrated before a motor program can be specified (e.g. Bullock & Grossberg, 1988). In theory, such computations can only occur, if both information sources are represented in the same frame of reference (e.g. Pouget, Deneve, & Duhamel, 2002). According to one influential model, the initial retinocentric representation of the target is assumed to be transformed in head-centered coordinates by comparing retinal signals with an internal representation of eye position. Next, body-centered target coordinates are calculated by combining head position signals with the head-centered representation. Finally, the location of the target and the location of the limb can be directly compared, since both pieces of information are in the same frame of reference (body-centered), and appropriate movement parameters can be generated (Flanders, Tillery & Soechting, 1992). This model is based mainly on a series of psychophysical studies, in which pointing movements to memorized target locations were made and spatial distributions of errors were analyzed. In contrast, Buneo et al. (2002) reported evidence from single cell recordings for a direct transformation scheme, in which the target position and the current hand position are integrated on the level of eye coordinates (see also Andersen & Buneo, 2002). The existence of both planning modes is supported by several findings (McIntyre, Stratta, & Lacquaniti, 1997, McIntyre, Stratta, & Lacquaniti, 1998, Carrozzo, McIntyre, Zago, & Lacquaniti, 1999) and some extensions and modifications were suggested (Bataglia-Mayer et al., 2003, McIntyre et al., 1998, Henriques, Klier, Smith, Lowey, & Crawford, 1998, Crawford, Medendorp & Marotta, 2004). However, exact mechanisms are still not thoroughly understood and seem to be task and context dependent (e.g. Bataglia-Mayer et al, 2003).
The importance of the underlying frames of reference was also recognized within an other line of research. Based on a considerable body of neurophysiological, neuropsychological and psychophysical evidence several authors proposed two distinct modes of sensorimotor processing (for reviews see Goodale et al., 2004, Jeannerod, 1997, Jeannerod et al., 1995,

Milner & Goodale, 1995, Norman, 2002, Paillard, 1991a,b, Rossetti & Pisella, 2002, Rossetti, 1998). The direct mode, labeled as “sensorimotor” (Paillard, 1991a), “pragmatic” (Jeannerod et al., 1995), or “vision for action / how” (Milner & Goodale, 1995) is assumed to deal with absolute metrics within an egocentric frame of reference und to extract parameters from sensory flow that are primarily relevant for generating a corresponding behavior. In contrast, the “representational” mode (termed also as “semantic”, “cognitive”, and “vision for perception”) is assumed to operate within an allocentric or an object frame of reference and enables to create an internal representation by binding stimulus attributes.

One of the essential aspects of the mentioned dissociation seems to be the time between stimulus and response (e.g. Rossetti & Pisella, 2002). Some observations in brain-damaged patients indicated selective impairments of immediate and delayed action control mechanisms. Goodale et al. (1994) investigated grasping movements of an agnostic patient (D.F.), whose perceptual discrimination performance was dramatically impaired. The authors reported that she shows an appropriate anticipatory scaling of her grasp only if objects were visible before movement initiation. This ability was lost if response was delayed by an interval of 2 seconds. Comparable results were obtained with a patient with tactile and proprioceptive deficits (Rossetti, 1998). In contrast, Milner et al. (1999) described an ataxic patient, whose pointing accuracy “paradoxically” improved when a delay of 5 seconds was used, as compared with immediate performance.

Further evidence for different delay dependent changes of motor planning and control processes stems from studies with normal subjects. Rossetti and colleagues reported a series of simple pointing experiments, in which delay was systematically varied (for review see Rossetti, 1998, Rossetti & Pisella, 2002). When movements were initiated immediately after the target presentation, the authors observed end point variability ellipses, main axes of which tended to be oriented in the direction of the movement. In contrast, delayed responses were associated with endpoint distributions, which were oriented towards other targets (orthogonal to the movement direction). Moreover, the delay dependent courses of the constant and variable errors showed a rapid change within the first second remaining relatively constant until a delay interval of 8 seconds (see also White, Sparks, & Stanford, 1994 for similar pattern of ocular errors in monkeys). Similar results were obtained, when subjects pointed to proprioceptivly defined targets.

The mentioned findings are typically interpreted as evidence for dissociation of brief representations lasting for a few seconds and which can be used for precise sensorimotor transformations from rather “cognitive” mechanisms involved in planning and controlling

delayed responses (for further evidence see Hu et al., 1999, Bridgeman et al., 2000, Bradshow & Watt, 2002, Elliott & Magdalena, 1987, Vaillancourt & Russel, 2002 and other studies in the above cited review articles).

Results from studies, which investigated the influence of optical illusions on perception and action mechanisms are often interpreted as further evidence for dissociation between "perception" and "action" mechanisms[15]. However, this research area revealed contradictory results (for discussion of this topic see Bridgeman, 2002, Glover, 2004, Norman, 2002, Rossetti & Pisella, 2002). This fact may indicate that if proposed dissociation between "sensorimotor" and "cognitive" modes makes sense, the corresponding distinction between "egocentric" and "allocentric" processing may not be critical (for similar notion see Carrozzo, Stratta, McIntyre, & Lacquaniti, 2002).

Apart from the suggested interpretation, the studies mentioned above show that characteristics of sensorimotor processes can change, dependent on time delay between a stimulus and a corresponding response. Thus, the question of sensorimotor transformation processes (e.g. in which frame of reference a current movement is planned?) can be referred to a broad research area concerning retention mechanisms in general.

It was repeatedly shown that a large portion of initial visual information decays within a few hundred milliseconds (see Sperling, 1960 for a pilot experiment). This early sensory storage ("iconic memory") is assumed to be associated with parallel processing, transmitting information about basic stimulus attributes and operating over several high capacity channels within a modality (for review see e.g. Massaro & Loftus, 1996). In contrast, retaining information over seconds to minutes ("short-term memory" or "working memory") was shown to include limited capacity, attention and categorization processes (for a review see e.g. Miyake & Shah, 1999). In addition, several findings indicated a further "transient storage" within the visual modality, which takes place between the early sensory and the classical short-term memory (Magnussen et al., 1998, Magnussen & Greenlee, 1999, Magnussen, 2000, Pasternak & Greenlee, 2005, Ruchkin et al., 2003). Magnussen and Greenlee (1999) reported a series of psychophysical experiments, in which the inter-stimulus interval was varied and delayed discrimination of basic stimulus attributes, like orientation or spatial frequency, was required. The authors obtained that the choice reaction times did not change during the first three seconds, while longer delays led to a strong increase, indicating an additional process after a few seconds. Based on these and similar results, the authors concluded that "perceptual on-line representations" are functionally and anatomically distinct

[15] Several findings indicated that optical illusions affect judgmental responses stronger than motor responses and that delay increases illusion effects on action.

from “classical” sensory and short-term memory processes. The perceptual storage was attributed to a set of post-categorical parallel feature-selective mechanisms, which were assumed to have limited capacity and to code basic dimensions of a visual stimulus. Following these findings, one may argue for at least two temporal markers within sensory retention mechanisms, if information must be maintained in the range of several seconds. Interestingly, 500ms (typical duration of iconic memory) as well as a few seconds intervals (approximate duration of on-line perceptual representations) are also considered to be critical for dissociation of “sensory-motor” from “cognitive” processing, which was described previously (e.g. Rossetti & Pissella, 2002, Westwood et al., 2001). This fact is not surprising since characteristics attributed to “sensori-motor” mechanisms are similar to those usually ascribed to “iconic memory” (precategorical, very short-term storage, unconscious, etc.), while “cognitive” processes are comparable with those of more “durable” storage (postcategorical, depend on attention resources, conscious, etc.). Thus, it seems to be useful to assume that depending on the time between the stimulus and the response, motor planning processes can include different information sources (or different representations of initially the same information). This assumption would be compatible with a recent neuroscience perspective of sensory-motor interactions, which suggest different hierarchical levels of perception-action integration (e.g. Fuster, 2001, 2004).

In the present study this proposal was tested by using EEG in a visuomotor task. By fixating a lighting point at eye level, the subjects performed one-dimensional hand movements to visual targets, arranged at different distances on a horizontal plane along the mid-sagittal axis of the trunk. Additionally, three delay conditions were implemented: the signal for movement initiation occurred 200, 1000 and 5000ms after the target offset. Analyzing ERPs (“evoked potentials”) we mainly focused on effects, which were associated with the manipulation of information type (i.e. with distance manipulation). Since direct comparison of delay conditions is difficult, especially during delay intervals, due to the different durations, and delay differences in comparable epochs may be a result of unspecific factors, like attention, we were mainly interested in delay dependent distance differences.

Furthermore, by using an kinesthetic matching task in one recent study, we obtained a distance specific modulation of an ERP component during movement execution. Our results suggested its essential role in the control of rapid hand movements. In the present experiment we aimed to replicate this finding and to provide further insight into electrophysiological correlates of movement control mechanisms.

4.2 Materials and methods

4.2.1 Subjects

Twenty-two right-handed, neurologically normal subjects participated in the present study. They received an honorarium or course credit at the end of the experiment. One subject was excluded from the analyses due to insufficient quality of kinematic and EEG data. The final sample included eleven males and ten females between 21 and 35 years of age (mean 25 years). None of the participants had any visual deficit except those corrected by lenses.

4.2.2 Paradigm and task

Apparatus

The subjects sat in front of a linear track device, allowing one-dimensional movements of a pen-like, lightly moveable handle on the horizontal plane slightly above the waist. Eight green LEDs with visible surface of 6 mm² were integrated at distances between 10 and 31 cm from the starting position (3 cm between successive LEDs) along the mid-sagittal axis of the trunk. The starting position was defined as the nearest possible handle location in respect to the body (approximately 10 cm). A fixation light (red LED with visible surface of 1 mm²) was mounted 70 mm in front of the subjects and its height was adjusted to the individual's eye level. The experiment was performed in total darkness, apart from rest periods, in which the room was illuminated and the vision of the whole device was occluded. Thus, the subjects were prevented from having visual contact to the apparatus.

Experimental procedure and design

At the beginning of a trial subjects positioned their head on an individually adjusted headrest and an auditory warning stimulus was presented (2000Hz). Two seconds later a red fixation LED was illuminated. After a fixed interval of two seconds, one of eight target LEDs was lighted for a period of 50ms. After a memory delay of 200, 1000, or 5000ms in respect to the target offset, the fixation light was extinguished, indicating that subjects should initiate the movement towards the remembered target position. After an interval of two seconds a second auditory stimulus was presented (250Hz) and subjects could return the arm to the starting position. The inter-trial interval was randomly varied between 3000 and 3350ms.

An 8 targets x 3 delays x 32 repetitions within-participants block-design was used. The experiment was divided into twelve blocks, each of them consisted of 64 trials (8 locations x 8 movements). The delay duration within each block was constant. Eight targets were randomly

presented with the constraint that the whole sequence of positions should be completed before another repetition. The order of blocks was also randomized for each participant. Each subject performed three practice blocks including all delay conditions. After each block a rest was made, the duration of which was adjusted to the individual's demand. An experimental session lasted between five and six hours including rest periods and electrode placements.

4.2.3 Recording and data preprocessing

Behavioral data

An ultrasound motion devise (ZEBRIS, CMS 20) was used to record the movement trajectories of the manipulandum. The data were sampled at 100 Hz initially and analyzed with a specially written software using Lab View codes (National Instruments, Graphical Programming for Instrumentation). Tangential velocity and acceleration were computed by using standard differentiation techniques. Movement onset was defined as the first time when position trajectory exceeded 5 mm. Maximal velocity and maximal acceleration values were determined for each trial. Trials with artifacts and with a movement onset which exceeded 1.5 seconds in respect to the "go signal" were excluded from further analyses.

EEG data

EEG data were recorded continuously from 61 scalp locations during task performance. A cap with an equidistant position montage was used (Easy cap, System Falk Minow, Montage Nr. 10, see Appendix 3-A). All scalp electrodes were initially referenced to the tip of nose and re-referenced offline to the average reference. Electrooculographic (EOG) activity was recorded from electrodes, placed vertically from above and below the left eye (vEOG) and horizontally from the outer canthi of both eyes (hEOG). Electrode impedances were kept below 5 kΩ. EEG and EOG were amplified between DC and 100Hz by using two 32 channel amplifiers (SYNAMPS, Neuroscan) and digitized with a sampling rate of 500Hz. DC drift was corrected according to Hennighausen et al. (1993). Eye movement artifacts were removed by application of the regression method suggested by Gratton et al. (1983), while trials with other artifacts were rejected based on a threshold criterion, allowing a maximum voltage range of 200 μV within a trial segment. Acquire software (NeuroScan) was used for collection and Brainvision Analyser Software (Brainproducts) for analysis of data.

Markers indicating target onset and offset of the fixation light were put online, while movement onset times were imported offline after the behavioral pre-processing stage.

4.2.4 Data analysis

Behavioral parameters

The following parameters were defined as dependent measures and analyzed statistically by using repeated measures analyzes of variance (ANOVAs) with target distance (8 levels) and delay (3 factors) as within-subjects factors:

a) Reaction times (time from offset of fixation light to the movement onset)
b) Constant error (mean deviation of the moved distance from the target distance)
c) Variable error (was computed according to: V = (SD / M)*100, where V – coefficient of variability, SD – standard deviation and M – mean moved distance within one experimental condition and one subject)
d) Peak acceleration
e) Peak velocity

Additionally, to explore processes taking place during movement execution, we performed a correlation analysis. There is evidence that some features of the movement trajectory are pre-planned before movement initiation and that early kinematic parameters like peak acceleration may be a signature for such central planning processes (e.g. Gordon & Ghez, 1987b, see also Messier & Kalaska, 1999). According to these findings, we computed Pearson's product moment correlation coefficients between the amplitude of maximal acceleration and the endpoint of movement position on a trial basis for each subject, in order to investigate the amount of pre-planning and of online corrections in the given experiment. For instance, an increase in this relation would indicate an increasing dominance of planning processes taking place before movement initiation and a decreasing role of on-line corrections. Possible changes, caused by experimental manipulation were tested with a two-way ANOVA with delay (3 levels) and distance (8 levels) as within-subjects factors.
For all analyses, significance was tested on an alpha level of 0.05 and degrees of freedom were adjusted according to Huynh and Feldt (1976).

EEG parameters

In order to draw conclusions about similarity or dissimilarity of processes taking place under different delay conditions, we followed the arguments mentioned in the introduction.
It was repeatedly shown that neuronal representation of information over short delays consists of transient activation of several distributed neuron populations within the cortex. However, not all of this activity can be ascribed to specific task-related information processing (for evidence from EEG research see e.g. McEvoy, Smith & Gevins, 1998, Gevins et al., 1996,

Gevins, Smith, McEvoy, & Yu, 1997). Analyzing ERPs in a working memory task by using verbal and spatial stimulus material, McEvoy et al (1998) could show that some components were sensitive to task manipulation (verbal vs. spatial), while others not (e.g. P300 response). Moreover, some other deflections were shown to be affected by the working memory load, but to be comparable in both tasks (e.g. frontal and parietal slow waves) possibly indicating mechanisms of attention demands.

Delay manipulation may be a priori assumed to be associated with a different amount of attention allocation. To limit the results only to ERP differences, which should be directly related to the content of the memory trace, we mainly focused on distance specific changes of evoked activity.

Initially, we defined three processing phases for further analysis: *encoding / delay*, *motor preparation* and *motor control*. According to this, the ERPs were adjusted to the stimulus onset (encoding / delay phase), to the offset of the fixation point (motor preparation) and to the movement onset (motor control). The baselines were determined as the averaged activity in the –100 to 0 ms interval preceding each trigger.

The goal of the statistical analyses was to identify time periods and locations, where the distance manipulation was associated with differences in the mean amplitude of the recorded evoked potentials. For this purpose we divided the defined processing phases in several time windows based on visual data inspection. Table 4-1 gives an overview of the used assignments.

Table 4-1: Time windows, which were specified as the basis for the statistical analyses. The times are depicted in ms in respect to the trigger of each processing phase. Note: due to different lengths of the delay duration, analyses of the late period of encoding / delay phase did not contain all delay conditions; X – was not included in the analyses.

Delay condition	**Encoding / Delay**								**Motor preparation**					**Motor control**							
	100-150	150-200	200-250	250-500	500-750	750-1000	1000-3000	3000-5000	0-100	100-200	200-300	300-400	400-500	0-50	50-100	100-150	150-200	200-250	250-300	300-350	350-400
“200”	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
“1000”	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-
“5000”	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Univariate repeated measures analyses of variance (ANOVAs) were conducted on the mean voltage amplitude of each time window by using algorithms generated by the general Linear Models procedure of SPSS (12.0).

While ERPs of all delay conditions in the early encoding phase as well as in the motor control phase appeared to be comparable, visual inspection of the motor preparation phase revealed quite different courses of the evoked activity dependent on delay condition[16].

On this account, we included all delay conditions in the initial statistical analyses in the early encoding and in the motor control phase and performed "time-window specific" ANOVAs with the within subjects factors "distance" (8 levels), "delay" (3 levels) and "electrode" (61). In contrast, in order to ensure comparability of used measures (mean amplitude) in the motor preparation epoch, we computed ANOVAs for each delay condition separately (within-subjects factors: distance (8 levels) and electrode (61 levels).

The analyses of the time windows between 500 and 1000ms after the stimulus presentation only contained two delay levels ("1000" and "5000"), and the interval between 1000-5000ms was analyzed by two-way ANOVAs due to the absence of comparable data of "200" and of "1000" delay conditions ("distance" and "electrode" as within subjects factors).

All analyzes mentioned above, provide information about time segments, in which significant differences between experimental conditions may occur, which could be expressed in significant "electrode" x "distance", "electrode" x "delay", "electrode" x "delay" x "distance", or "delay" x distance" interactions. Since we were mainly interested in effects caused by the distance manipulation, we performed "electrode specific" ANOVAs only for time windows, where distance effects became significant[17].

In the case of the motor preparation phase, we treated each delay condition separately again and computed one-way ANOVAs with the within-subjects factor "distance" (8 levels) for each delay condition and each electrode[18]. Other processing phases were analyzed by using two-way ANOVAs ("distance" and "delay" as factors) for each electrode. In order to give a complete picture of the effects, we plotted the significant F values of the main effects "distance" derived from "electrode specific" ANOVAs as topographic maps.

For all statistics significance was accepted at the conventional level of probability (0.05) and all tests were adjusted for nonsphericity according to the formulae of Huynh and Feldt (1976). Moreover, some additional measures were applied for analyses of the early phasic activity, mentioned above, and of the ERPs in the motor control phase. The details are reported in the result section.

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[16] Especially the shortest delay condition showed a quite different dynamic, where a pronounced phasic activity over posterior recording sites was observed, see also results and discussion.

[17] If it appeared to be useful some other results were also presented.

[18] Similar procedure would be appropriate for "5000" delay condition in a time range between 3000 and 5000 ms of the delay phase. However, no significant effects were found in the superordinate statistic for this time window making "electrode specific" analysis unnecessary.

4.3 Results and discussion

4.3.1 Behavioral data

The averaged position, velocity and acceleration trajectories of 24 experimental conditions are shown in Figure 4-1 (top). These kinematic parameters had typical characteristics like single-peaked bell-shaped velocity profiles, biphasic acceleration and linear position courses. An increase in distance was associated with a significant increase in maximal acceleration and velocity values in each delay condition (see middle part of Figure 4-1 for means and Table 4-2 for statistical results). Moreover, both measures were also affected by the delay manipulation as indicated by the corresponding significant main effects (Table 4-2). The longer the delay the lower were the peak values of acceleration and velocity. Post hock tests indicated that only the shortest and the longest intervals differed significantly from each other in both cases ($p < .05$).

The subjects showed on average a clear tendency to undershoot the target distance as indicated by the constant error measure (Fig. 4-1; 0 means no error or correct reproduction). This tendency increased significantly with target distance (significant main effect of "distance", see Table 4-2). In contrast, the variable error (coefficient of variability) decreased significantly when the distance became longer (Table 4-2). Although a slight trend towards more underestimation of the distance in longer delay conditions and a tendency to a higher variability with an increase of delay duration were detectible (Figure 4-1), delay effects did not reach the significance threshold (Table 4-2).

The analyses of the reaction times revealed a significant "distance x delay" interaction, suggesting delay dependent changes of distance differences (see Figure 4-1 for means and Table 4-2 for statistical results). Only marginal changes across eight target distances were detectible in two longer delay conditions. In contrast, during the shortest delay condition, the middle target positions showed a pronounced decrease in reaction times as compared with the nearest and the most distant targets.

Table 4-2. Main effects and Interactions of performed ANOVAs, *p<.05; **p<.01. All tests were adjusted according to Huynh and Feldt (1976).

	"delay"			"distance"			"delay x distance"		
	df	F	P	df	F	P	df	F	P
Peak acceleration	2,40	**11.32****	**<.001**	7,140	**44.40****	**<.001**	14,280	.52	.804
Peak velocity	2,40	**8.18****	**.003**	7,140	**94.73****	**<.001**	14,280	.86	.503
Constant error	2,40	1.17	.313	7,140	**11.11****	**.002**	14,280	1.01	.412
Variable error	2,40	2.17	.128	7,140	**15.22****	**<.001**	14,280	.82	.608
Reaction times	2,40	1.09	.341	7,140	**2.42***	**.031**	14,280	**3.71****	**<.001**

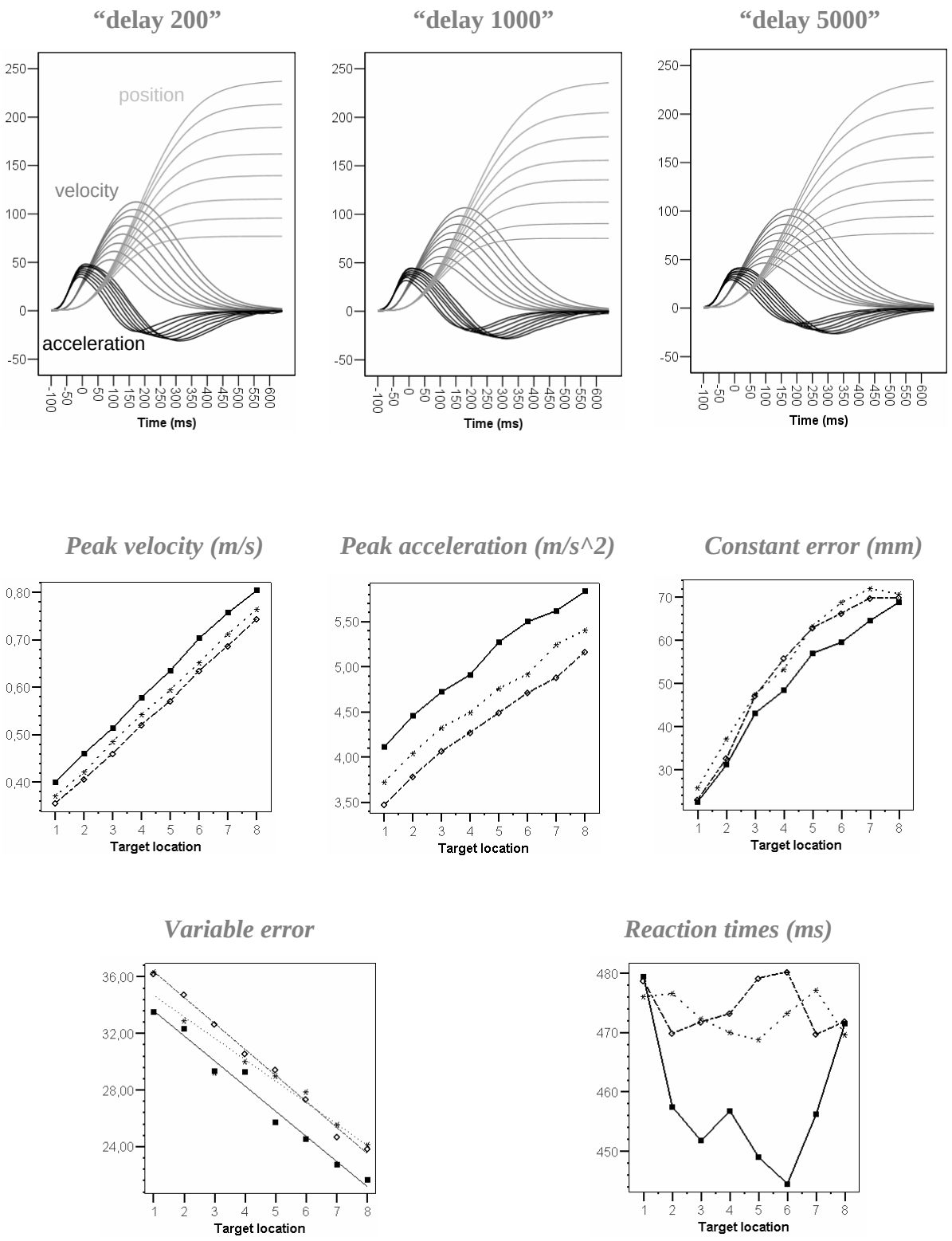


Figure 4-1. *Top:* Kinematic parameters of movements averaged for all subjects and each experimental condition. All curves were synchronized to movement onset as defined in the method section and scale units of the Y axis are mm (position), 150 x m/s (velocity) and 10 x m/s^2 (acceleration). *Middle:* Averaged values of peak velocity, peak acceleration and constant error (positive values reflect the magnitude of underestimation). *Bottom:* Mean coefficients of variability (variable error) and reaction times. Note: ■ = "delay 200", ✳ = "delay 1000", ◇ = "delay 5000" conditions.

Discussion

Analyses of early kinematics revealed distance and delay dependent changes of these parameters. We observed a gradual increase in maximal acceleration and velocity values with an increase in distance. This result is in line with several previously reported findings (e.g. Gordon, Ghilardi & Ghez, 1994, Messier & Kalaska, 1999).

As time delay increased, peak acceleration and peak velocity tended to decrease. A similar finding is reported by Goodale, Jakobson, and Keillor (1994), who obtained a decrease in maximal velocities of grasping movements if delay intervals of two and 30 seconds were implemented, as compared with grasping of visible targets (for evidence of delay dependent kinematic changes see also Hu et al., 1999). However, to what extent these changes can be attributed to different or comparable processing modes (perceptual fading, noise vs. qualitatively different systems) cannot be determined from the current data.

An increase in target distance was also associated with an increase of undershooting bias. A similar pattern of results was often reported in visual pointing tasks, when visual feedback is prevented during pointing (e.g. Chieffi, Allport, & Woodin, 1999, Lemay & Proteau, 2001). It was suggested that this “distance” effect may arise from errors in the sensorimotor transformation from visual representation of the target location to body-centred coordinates (Soechting & Flanders, 1989). In the present study we did not find any significant differences across three delay conditions relating the constant error, possibly indicating similar transformation processes mentioned above (but see ERP results).

In contrast to the constant error, response variability, as measured by the used coefficient of variability, decreased with an increase in movement amplitude. We assume that this result may reflect an increase in sensory noise originating from a decrease in localization efficiency of the visual system with target eccentricity. In one of our previous studies we obtained a comparable result in a motor matching task, where a first hand movement was mechanically stopped at an unpredictable location. According to our analyses, a first (encoding) movement was planned aiming by default at a far position. Mechanical movement breaking was assumed to cause a “conflict” between the actual and the expected target location, which should be reduced with an increase in distance. Decreased response variability (measured as standard deviation) when target distance increased was interpreted as a result of changes in encoding efficiency associated with the already mentioned conflict. The results from the current experiment seem to be comparable with these findings.

By analysing reaction times we discovered that during the shortest delay conditions, the subjects initiated the movement faster than during the other conditions. However, this effect

was restricted to the middle target positions. We assume that under time pressure, the subjects prepared some default motor response to one of the central target positions and had to adjust this response if the real target deviated from the expected position. Evidence for such processes is reported by Ghez and colleagues (see e.g. Ghez et al., 1997). In a series of studies the authors could show that before specific information about a variable target location is available, subjects set default values for amplitude and direction based on expectations. Moreover, in respect to the amplitude, the default seems to be set in the middle of the target range.

However, if response was delayed, the subjects did not show similar patterns, possibly indicating other motor planning strategies.

4.3.2 Event related activity[19]

An overview of the measured event related activity in the three delay conditions is given in Figures 4-2 and 4-3 (see also Appendix 4-A,4-B and 4-C for another type of illustration). The ERPs were characterized by early phasic responses following the target onset with pronounced negative peaks over parietal to frontocentral and positive deflections mainly localized at lower occipital sites. In the two longer delay conditions these first bursts of activity were followed by large negative waves at frontal electrodes probably corresponding to the early part of CNV ("orientation wave" of "Contingent Negative Variation") and positive deflections at posterior recording sites, which we attributed to LPC ("late positive complex"). Additionally, a pronounced rhythmic activity over occipital and parietooccipital regions was detectible during all delay conditions in the time range between approximately 100 and 600 ms after stimulus presentation ("evoked alpha activity", see also section 4.3.2.1). In the "5000 ms" condition, a "classical" CNV ("expectancy wave") with negative maxima over frontal and frontocentral regions occurred at the end of the delay interval. As far as the ERPs of the three delay conditions were comparable, no visible differences in respect to the wave courses as well as to the voltage distributions across the scalp were detectible. The visual inspection of the ERPs during movement executions revealed similar results (see Figures 4-2 and 4-3). Although the absolute amplitude of measured deflections seemed to decrease with an increase of delay duration, the whole voltage topography did not indicate substantial changes: a positive maximum over frontocentral regions and negative deflections over parietal areas were present in all delay conditions.

However, after extinguishing the fixation light, the ERPs showed a highly delay dependent characteristic. Although similar negative deflections were obtained in all delay conditions shortly before the movement onset (that we referred to as "motor potential"), the dynamics as well as scalp distributions, were quite distinct in this processing phase.

During the "delay 200" condition we obtained rhythmic deflections at posterior electrodes ("evoked alpha activity"). Moreover, in contrast to both other conditions no distinct groups of potentials were observed and voltage topography seemed to change only in magnitude in this processing phase. ERPs in the "1000 ms" condition mainly consisted of two groups of deflections with quite different topography. In addition to the negative shifts, which we labeled as "motor potential", phasic responses mainly localized at occipital sites were obtained. Interestingly, the topography of the occipital deflections was quite similar to the

[19] In order to describe data we adopted some labels of known components obtained in similar recording situations.

topography of positive maximums during encoding between 500 and 1000 ms after the target onset.

In contrast, the signal measured during the “5000” ms condition was more complex and showed at least one additional group of waves temporally located between components identified in the 1000 ms condition. This fact is also evident in the voltage distributions, especially in the time range between 300-400ms after the “go signal”, where a broad parietal activity is present.

In summary, the visual data inspection revealed rather similar evoked activity in the encoding phase, as far as delay conditions were comparable, as well as in the motor control phase. However, pronounced differences were obtained during the motor preparation phase.

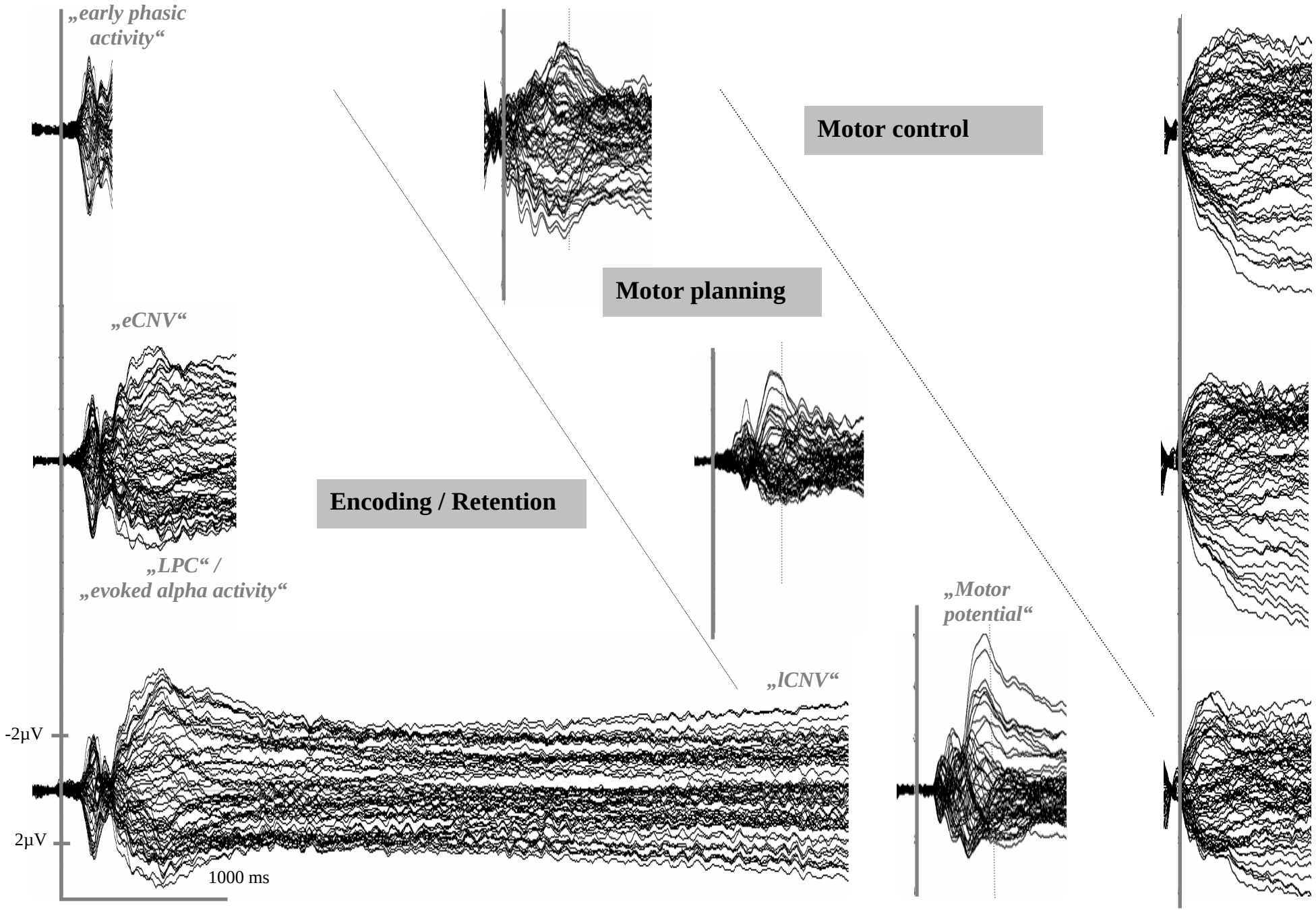
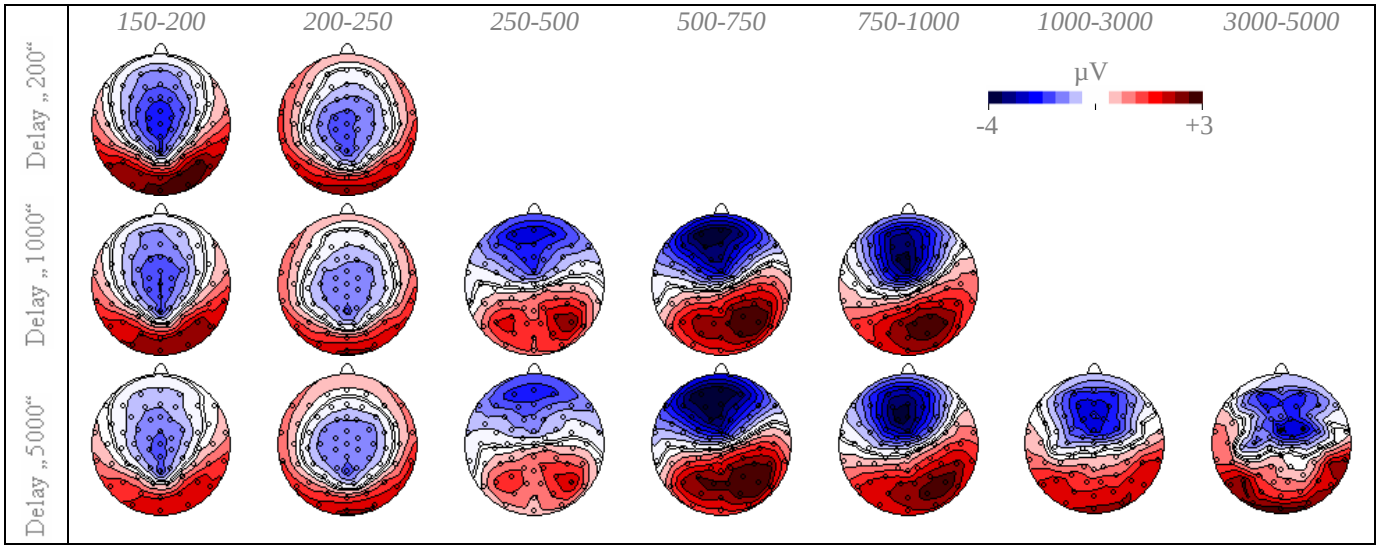
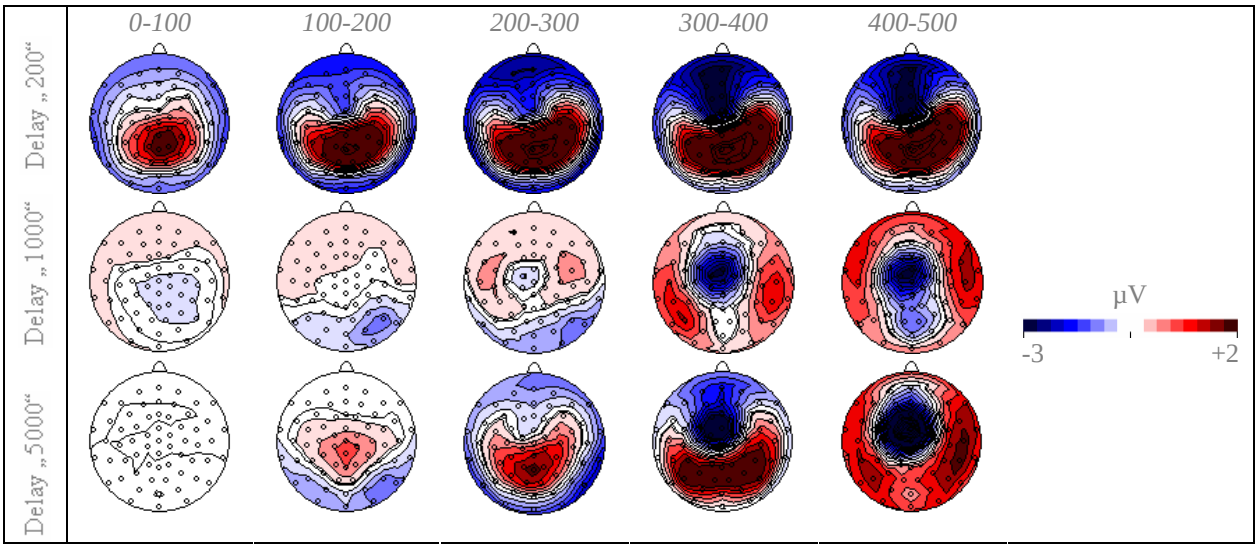


Figure 4-2. Over eight distance conditions averaged ERPs of three delay conditions. The Figure shows measured activity at all 61 electrode locations separated according to the defined processing epochs. Note: all ERPs were adjusted to triggers corresponding to the processing epoch and baseline corrected (-100/0ms) to emphasis epoch specific dominant activity. Vertical dotted lines reflect the mean onsets of movements.

(A)Encoding



(B) Motor planning



(C) Motor control

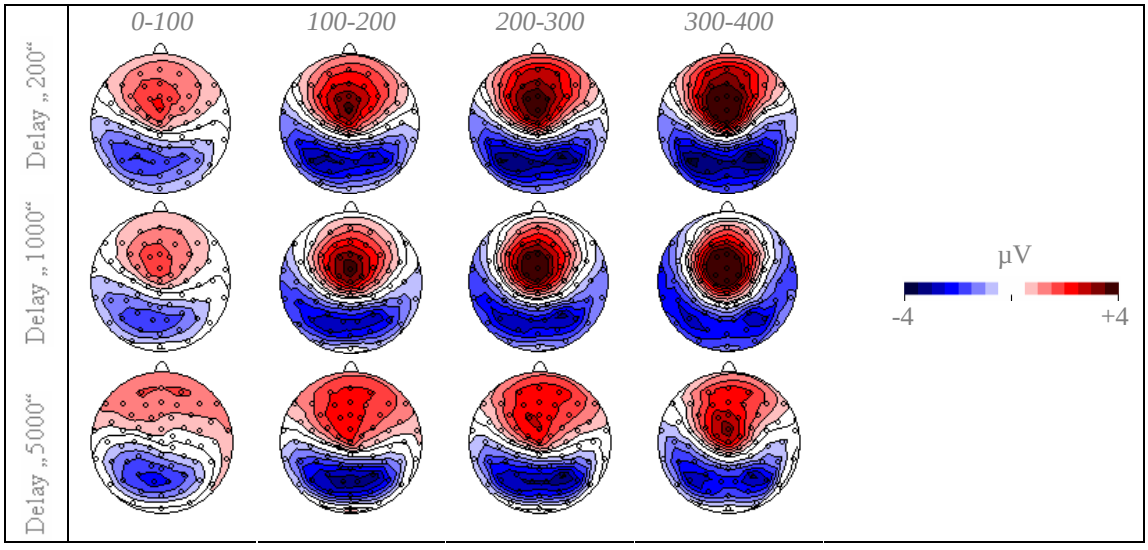
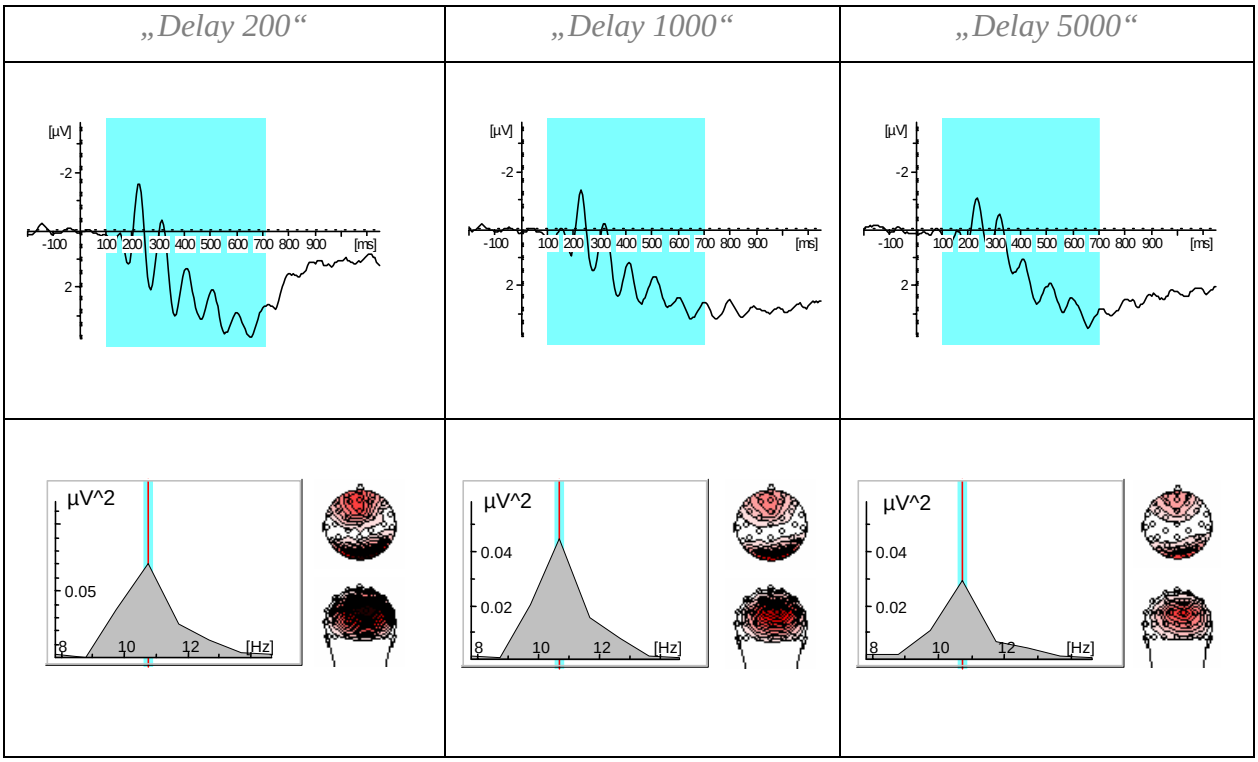


Figure 4-3. Over selective time windows and eight distance conditions averaged evoked activity of three delay conditions in three processing epochs.

4.3.2.1 Evoked alpha activity

Visual data inspection of ERPs revealed phasic deflections lasting several hundred milliseconds after the target presentation at posterior recording sites. This rhythmic activity was present in all delay conditions with an obvious frequency in the alpha range (8-12Hz). The over all subjects and distances averaged evoked potentials of three delay conditions at electrode PO4 are shown in Figure 4-4 (top). To define the dominant frequency of the mentioned signal changes, we computed three FFT ("Fast Fourier Transformation") analyses on grand average data, in which the over all subjects and all distance conditions averaged ERPs were included (absolute power values were calculated for each electrode by using Hanning window). The bottom part of Figure 4-4 illustrates some selected findings. According to the visual data inspection, a clear power peak in the alpha band range (10.7 Hz) was detectible in all delay conditions[20]. Electrode locations with maximal power values were found over posterior areas and were comparable during all delay conditions.



[20] Besides alpha activity, low frequencies also reached high power values. However, we were mainly interested in alpha activity and did not consider other frequencies here.

Figure 4-4. *Top*: ERPs at electrode PO4 in three delay conditions; marked range indicate segments used for FFT analyses. *Bottom:* Results of the FFT analyses for electrode PO4 and topographical maps indicating distributions of power values across electrodes in alpha frequency range (μV^2: 0 0.06).

We analyzed this evoked alpha activity by applying a band-pass filter (8-12Hz, slope = 12 dB/oct) to individual ERPs averaged over single trials and by computing the "Global Field Power" (GFP) courses in the chosen frequency range between –200 and 1000 ms in respect to the target onset. GFP corresponds to the root-mean-square deviations between all electrodes in a given potential field and can be used to describe how the field strength varies over time (e.g. Skrandies, 1995).

Figure 4-5 shows filtered ERPs of eight distance conditions at electrode PO4 (A), averaged for all subjects and delay conditions, and corresponding GFP curves[21] at the same location (B).

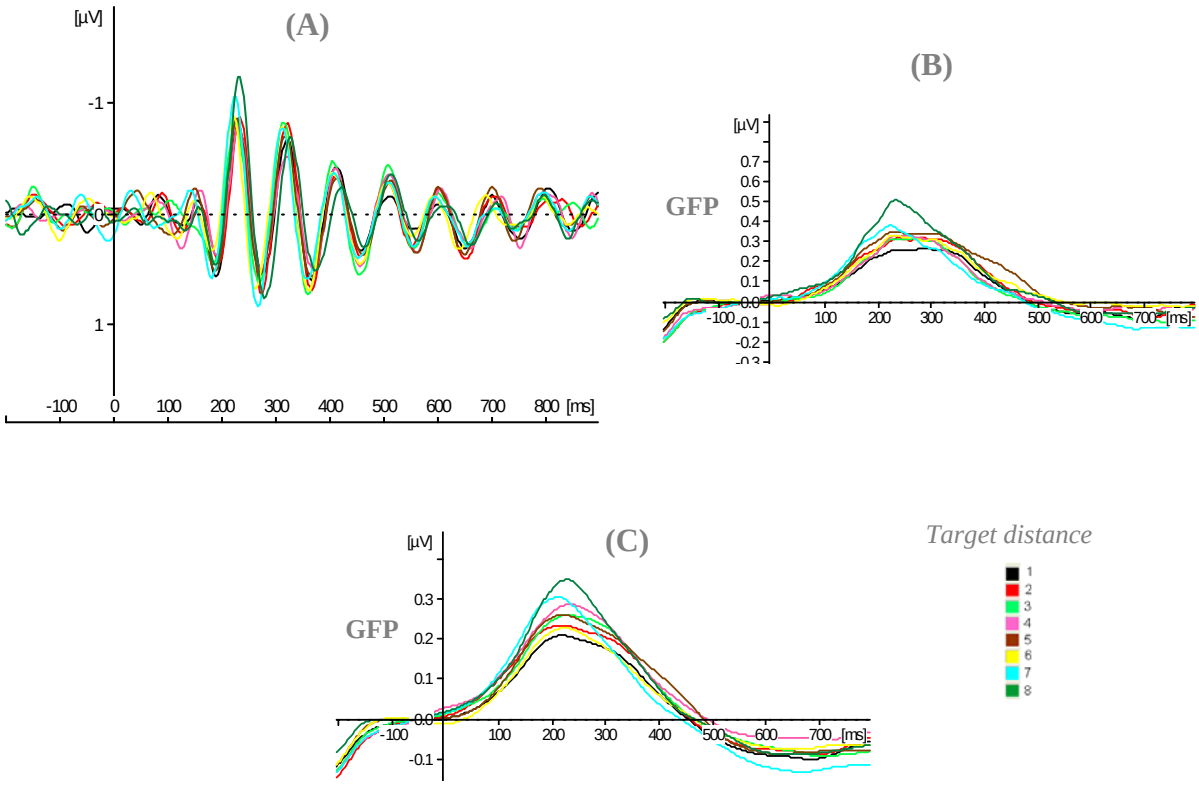


Figure 4-5. (A): Grand average ERPs of eight distance conditions after the band-pass filtering (8-12 Hz) at PO4; (B): Results of RMS analyses performed on individual ERPs at PO4 and averaged for all subjects according to eight distance locations; (C): GFP results performed on mean activity of eight neighboring posterior electrodes (see text). Note: prior to averaging, all GFP were baseline corrected (-100 - 0); for descriptive purpose GFP curves were filtered (3Hz low-pass filter).

[21] For GFP courses time interval between –100 and 0 ms in respect to the target onset was used as baseline.

Pronounced alpha activity was present in the time range between approximately 100 and 500 ms after stimulus onset and was obviously influenced by the distance manipulation at the given electrode. To check validity of the results performed with one single electrode, we computed a GFP analysis including eight neighboring locations, showing high power values in the alpha range (P3, P4, PZ, PO3, PO4, O1, O2, OZ; see Figure 4-5, C). Apart from a generally slightly reduced field power, the time course of alpha activity as well as distance differences were similar to those obtained at PO4.

We compared mean field strengths of experimental conditions in the time range between 150 and 300ms after stimulus onset including both, a single electrode data (PO4) and mean GFP of eight posterior locations. First, we computed two ANOVAs including only "extreme groups" of factor distance (distance "1" and "8") and all levels of factor "delay" ("200", "1000", "5000"). The corresponding results are shown in Table 4-3.

Table 4-3: Statistical results of two ANOVAs performed on mean GFP between 150 and 300 ms after stimulus onset including (A) only the electrode PO4, (B) eight electrodes (P3, P4, PZ, PO3, PO4, O1, O2, OZ). Note: Within subjects factors are "delay" (3 levels: 200, 1000, 5000) and "distance" (2 levels: "1" and "8"); All tests were adjusted according to Huynh and Feldt (1976). *p<.05; **p<.01

	"delay"			"distance"			"delay x distance"		
	df	F	P	df	F	P	df	F	P
(A)	2,40	2.00	.157	1,20	**10.60****	**.004**	2,40	1.54	.228
(B)	2,40	1.58	.220	1,20	**17,89****	**<.001**	2,40	.81	.453

Both analyses revealed a highly significant main effect for factor "distance", indicating that mean GFP of the alpha activity evoked by the eights target location was significantly higher as the mean GFP associated with first target location. None of the other effects became significant.

In the subsequent analyses we performed two ANOVAs again (with "delay" (3 levels) and "distance" (8 levels) as within-subjects factors) including all distance conditions. Table 4-4 summarizes these results.

Table 4-4: (see text for details)

	"delay"			"distance"			"delay x distance"		
	df	F	P	df	F	P	df	F	P
PO4	2,40	5.65**	.007	7,140	1.46	.207	14,280	.80	.634
Eight el.	2,40	5.45**	.008	7,140	1.87	.111	14,280	.89	.550

The main effect "distance" did not reach the significance threshold in both analyses. But, linear contrasts of factor "distance" became significant, indicating a trend towards a linear increase in GFP with an increase in distance (*PO4*: F = 5.98, P = .024; *Eight electrodes*: F =

7.17, P = .014). Figure 4-6 shows mean field strengths of all experimental conditions in the time range chosen for analyses. Despite a rather high variability of the data, a trend towards the mentioned direction was clearly detectible.

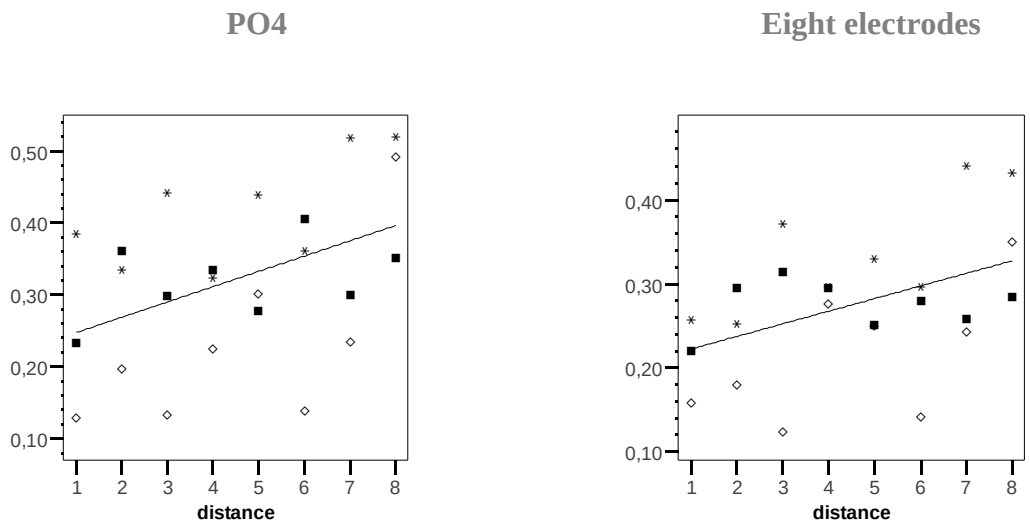


Figure 4-6. Mean values of GFP in 24 experimental conditions between 150 and 300 ms after the target presentation: *Left* - at electrode PO4, r*ight* - averaged over eight locations (see text). Note: ■ = "delay 200", ✳ = "delay 1000", ◇ = "delay 5000" conditions.

Discussion

By analyzing the early phase locked phasic activity after stimulus presentation, we obtained an increase of power in the 10 Hz range in respect to a prestimulus baseline in all experimental conditions at posterior electrode sites. These results are not inconsistent with alpha desynchronization (decrease of alpha power) typically obtained after a sensory stimulation like Klimesch, Doppelmayr, Roehm, Pöllhuber, and Stadler (2000) nicely demonstrated[22].

If phase locked activity is analyzed, such bursts of evoked alpha activity in / over primary sensory areas are often reported in response to different kinds of sensory stimulation in higher mammals and human subjects (for review see e.g. Schürmann & Basar, 2001, Dinse et al., 1997, Basar, Schürmann, Basar-Eroglu, & Karakas, 1997). However, they seem to occur only if adequate stimulation is applied (i.e. in response to visual stimulation, evoked alpha rhythm is obtained in early visual areas, while auditory stimuli lead to alpha activity in auditory

[22] Both phenomenon occur in a similar time window at different recording sites and were attributed to different functions. Enhancement of evoked alpha activity probably arises due to a phase resetting after sensory stimulation, while total power typically decreases if measurements of event-related band power are used. See also Herrmann, Grigutsch, and Busch (2005) for discussion of this topic.

cortex), indicating their role in primary sensory processing (e.g. Schürmann, Basar-Eroglu, & Basar,1998). These 10 Hz oscillations last only a few hundreds milliseconds and are assumed to be associated with early sensory retention mechanisms, which keep information available over a short period of time (Basar 2005, Dinse et al., 1997, see also Ruchkin et al, 2003 for similar suggestion[23]). In case of the visual modality, such functions are attributed to the so-called "iconic memory" that operates in a similar time window and is associated with parallel and precategorical processes transmitting information about basic stimuli attributes (see e.g. Massaro & Loftus, 1996 for review of sensory memory).

Moreover, evoked alpha activity was shown to be dependent on local areal and modality specific factors, as well as on stimulus features indicating information specific processing rather than a global unspecific response to a stimulus (Dinse et al., 1997). These findings seem to be consistent with a hypothesis, recently proposed by Klimesch, Sauseng, & Hanslmayr (2005) that states that alpha ERS (event related synchronization) do not reflect "unspecific" inhibition, but rather a highly specific top-down process, which enables high information selection.

In the current experiment we detected small, but systematic differences in the amplitude of evoked alpha activity across eight target conditions at occipital and occipitoparietal electrodes. According to the findings mentioned above, we assume that the distance specific changes of the obtained phasic deflections may be associated with early content specific retention mechanisms operating on a low level of information processing and may be related to the "iconic memory store".

[23] Based on a review of several human ERP studies using visual stimuli, the authors (Ruchkin et al.) related early phasic responses over posterior areas to iconic store mechanisms. However, an exact frequency range of obtained oscillations is not reported.

4.3.2.2 Encoding / delay phase

Table 4-5 summarizes the major results of the “time window specific” ANOVAs in the given processing epoch.

Table 4-5: Selected results of ANOVAs performed on mean amplitude of respective time window with “distance”, “delay” and “electrode” as factors. Note: all tests were adjusted according to the method suggested by Huynh and Feldt; depicted degrees of freedom are not corrected, while probabilities represent corrected values;
* p(F) <.05, ** p (F) < .01.

Time window	„electrode x delay“			„electrode x distance“			„delay x distance“			“electrode x delay x distance“		
	df	F	P	df	F	P	df	F	P	df	F	P
100-150	120, 2400	**1.83***	**.046**	420, 8400	1.24	.182	14, 280	.40	.964	840, 16800	1.31	.087
150-200	120, 2400	**7.36****	**<.001**	**420, 8400**	**2.74****	**<.001**	14, 280	.67	.777	840, 16800	1.12	.277
200-250	120, 2400	1.06	.395	**420, 8400**	**2.13****	**.003**	14, 280	.73	.722	840, 16800	1.18	.191
250-500	60, 1200	**5.02****	**<.001**	**420, 8400**	**1.60***	**.019**	7, 140	.80	.584	420, 8400	.85	.695
500-750	60, 1200	.98	.423	**420, 8400**	**2.45****	**<.001**	7, 140	.41	.880	420, 8400	1.16	.276
750-1000	60, 1200	1.13	.348	**420, 8400**	**2.89****	**<.001**	7, 140	.15	.992	420, 8400	**1.73***	**.014**
1000-3000	-	-	-	420, 8400	.970	.524	-	-	-	-	-	-
3000-5000	-	-	-	420, 8400	.934	.580	-	-	-	-	-	-

As can be seen, manipulation of the stimulus distance produced significant effects in five of the eight time segments chosen for analyses. Apart from the interval between 750 and 1000 ms distance differences were independent from the delay manipulation as indicated by corresponding non-significant “delay x distance” and “delay x distance x electrode” interactions. Moreover, “delay x electrode” interaction became significant in three time windows, indicating mean amplitude differences between delay conditions. However, due to the non-significant “delay x distance” and “electrode x delay x distance” interactions, we do not have to consider them further (according to the reasoning described in the method section).
Electrode sites at which the mean amplitude was significantly influenced by the distance manipulation in the range between 150 and 750 ms are shown in Figure 4-7 (middle part).

The different distances caused broadly distributed differences shortly after the stimulus presentation (150-200ms), which were maximal over frontocentral and posterior areas. At these locations the effects consisted of an increase in activity with an increase in distance. A similar trend was observed in the next time window, where maximal differences were present at parieto-occipital electrodes and were expressed in stronger phasic responses the longer the distance was. The effect distribution resembles the topography and effect direction of evoked alpha activity analyzed in the previous section, and probably refers to the modulation in its

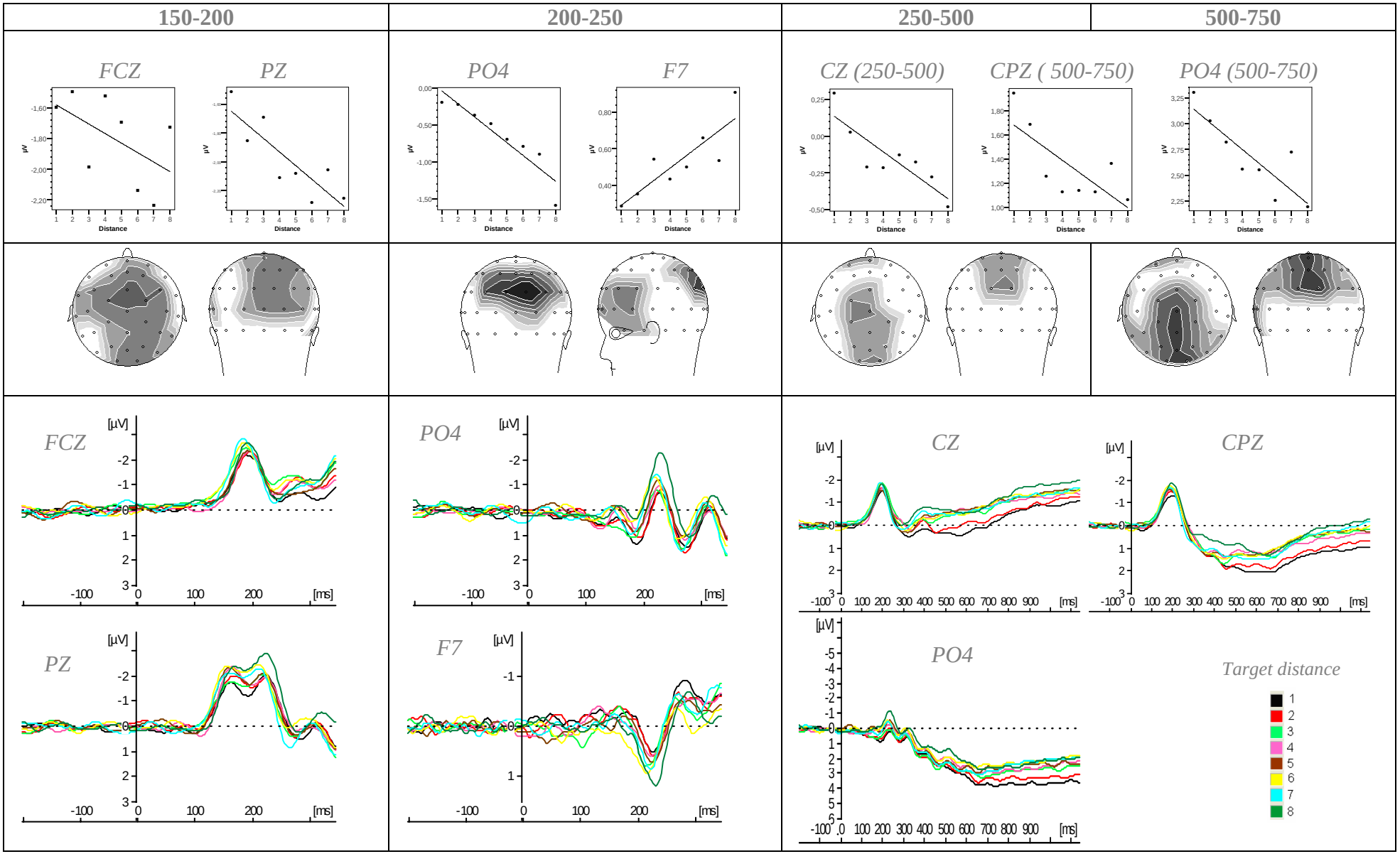

150-200
200-250
250-500
500-750
FCZ
PZ
PO4
F7
CZ (250-500)
CPZ (500-750)
PO4 (500-750)
Distance
μV
[μV]
[ms]
-100
0
100
200
300
400
500
600
700
800
900
Target distance
1
2
3
4
5
6
7
8

Figure 4-7: *Top*: mean voltage values at selected electrodes with the high F scores in a given time window. *Middle*: significant electrode specific F values for main effects of factor "distance" (0 6). *Bottom:* ERPs at selected locations. For descriptive purpose the ERPs were low-pass filtered (150-250ms = 20Hz; 250-750ms = 5Hz).

initial range. Somewhat weaker effects were obtained over left frontal sites, where an increase in distance elicited an amplitude increase in a positive wave.

In the range between 250 and 750 ms after stimulus onset significant distance differences occurred along the midline electrodes from parieto-occipital until central regions. They consisted of an amplitude increase of positive deflections over posterior areas with a decrease in stimulus distance. In addition, if the distance got longer we obtained a tendency towards higher negativity over central areas.

Analysis of the variance between 750 and 1000 ms provided delay and electrode dependent distance differences as indicated by a significant "delay x distance x electrode" interaction" (see Table 4-5). During the delay "1000" condition, the distance manipulation caused ERP effects, which were mainly localized at parieto-occipital and anterior frontal electrodes (see Figure 4-8). At anterior locations there was a trend towards an amplitude decrease of a negative deflection with an increase of distance until the middle target positions (e.g. Follow Bonferroni corrected post hoc comparisons at AFZ reached significance: 1vs.4, 1vs.5, 1vs.6, 1vs.7, 2vs.5). Similarly, at posterior locations a decrease of positive activity until target position "5" was obtained if distance got longer, with no further amplitude modulation in other distance conditions (e.g. significant differences at PO3: 1vs.3, 1vs.4, 1vs.5, 1vs.6, 1vs.7, 1vs.8, 2vs.5).

In contrast, the "5000" delay condition was associated with left frontal and central clusters of significant F values for factor "distance" (see Figure 4-8). As the distance increased, a trend towards an increase of negative amplitude was observable over left frontal areas, while central differences were rather expressed in a decrease in positive activity with an increase in the distance length.

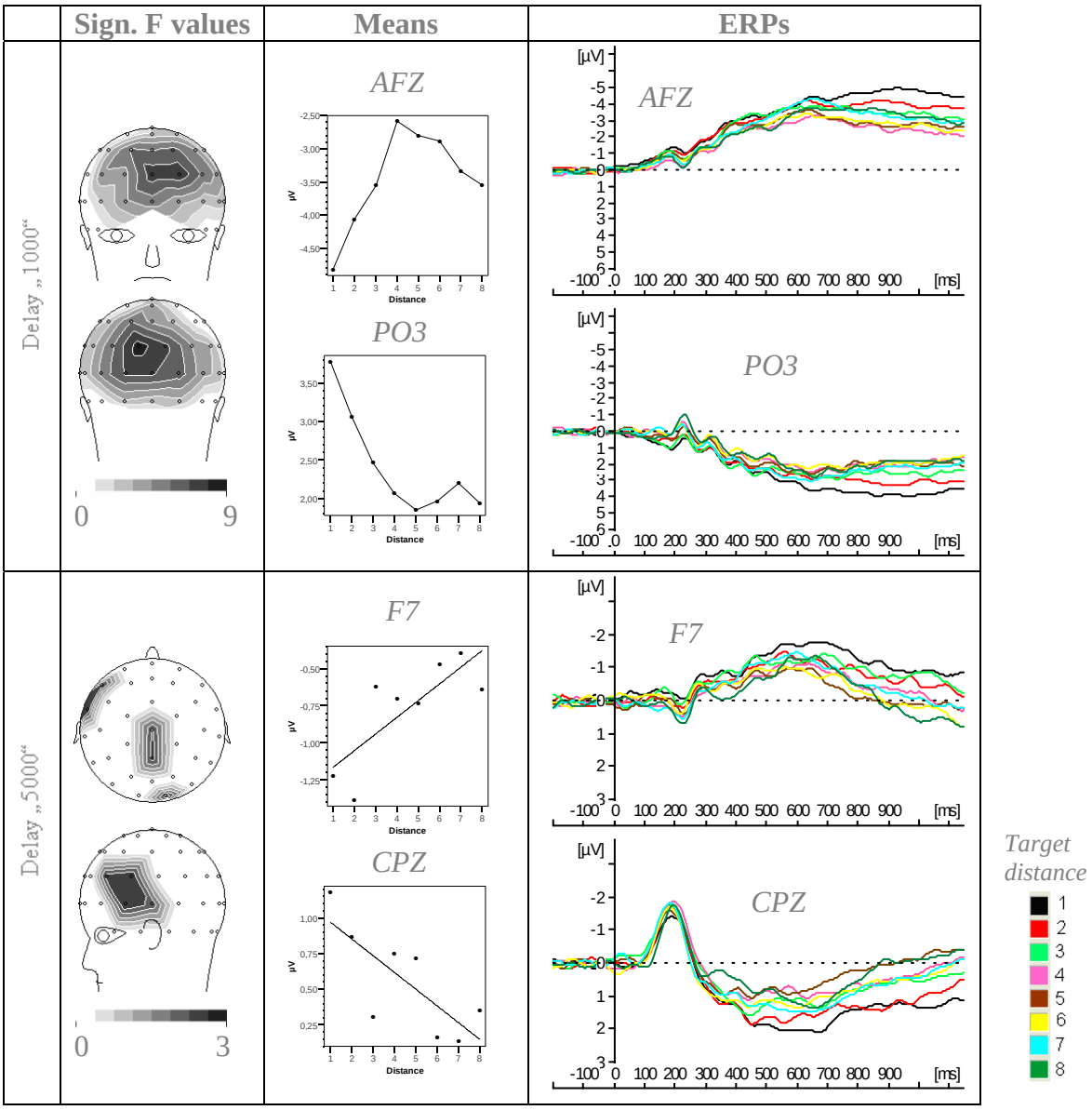


Figure 4-8: *Left:* F values distribution for factor “distance”, computed for delay “1000” and “5000” conditions separately; *Middle:* mean voltage values at selected electrodes; *Right:* ERPs at selected locations. All ERPs were filtered with low-pass filter (5Hz).

Discussion

Until 250 ms after stimulus onset, all delay conditions showed similar distance specific changes of the ERP amplitude (due to the absence of significant “delay x distance” and “delay x distance x electrode” interactions). We obtained a series of broadly distributed phasic deflections with local maxima over frontocentral and posterior regions in response to target presentation in this early processing phase. Some of them were significantly affected by the distance manipulation showing an increase in activity if target distance was extended. This pattern of results may indicate that early detection and / or encoding processes were

successively more effective the further the target location was, due to an increase in sensory sensitivity with a decrease in retinal eccentricity (see e.g. Klein & Levi, 1987, Rousselet, Husk, Bennett, & Sekuler, 2005).

Analyzing ERPs between 250 and 750 of the delay "1000" and delay "5000" conditions, we did not find delay specific distance effects again (corresponding interactions were not significant). Thus, the eight target distances modulated the ERP amplitude in both delay conditions similarly and were maximal at the midline electrodes over central and posterior regions. While ERP differences at central sites followed a similar trend described above (increasing activity with an increase in target distance), activity over posterior regions was enhanced at near targets as compared with far distances.

Posterior activity was characterized by positive deflections showing typical features of well known "late positive complex" (LPC). Positive activity over centroparietal and parietal regions probably reflects the "classical P300" (labeled also as P3 or P3b). This component was obtained in several modalities and in diverse stimulus conditions, in which a classification of events or stimuli into two or more categories was induced. The relation of this component to memory processes was extensively studied (for review see e.g. Rugg, 1995, Fabiani et al., 2000). Its amplitude proved to be sensitive to stimulus probability, processing resources demanded by a particular task and amount of information extracted from the event among others (e.g. Coles & Rugg, 1995; Fabiani et al., 2000, Johnson, 1986).

One finding in this research domain is that the amplitude of P3 became strongly reduced when subjects were asked to "ignore" some stimuli, suggesting an increase in P300 amplitude when more attention is invested on a task. An increase in perceptual and / or memory load contrariwise, which should result in an increase in resource demands, is often expressed in a decrease in P300 amplitude (see e.g. Kok, 2001 for discussion of this topic). However, there is also evidence for an inverse relationship between P3 amplitude and perceptual / cognitive resource demands in dual task situations, where P3 amplitude to primary task events increases with task difficulty (Fabiani et al. 2000, see also Donchin & Fabiani, 1991).

Based on an extensive review of P 3 findings, Kok (2001) suggested that the attentional capacity invested in the categorization of events is the main factor determining the modulation of P3 amplitude. A decrease in amplitude with an increase in task difficulty is assumed to result from a depletion of resources due to processes interfering with the categorization of events[24] (e.g. associated with memory search).

[24] Positive relation of P3 amplitude to attention, and an inverse relation to task difficulty is also predicted by Verleger (1988). P3 amplitude was also referred to as an index of capacity for processing task relevant stimuli by Wickens, Kramer and Donchin (1984).

In the current experiment we obtained an increase in P300 amplitude with a decrease in distance. According to the findings this result seems to indicate that during early encoding and / or categorization processes, attentional demand increased when distance decreased[25]. Since eight target conditions differed mainly in retinal eccentricity, we assume that perceptual identification and / or categorization processes are more difficult the closer the target was and thus may require more / additional resources (due to a decrease in spatial sensitivity).
In addition to the P3b, we obtained further positive deflections posterior to the P3b (sometimes labeled as "positive slow waves"). Similar components were obtained in diverse task situations, where spatial and / or object forms had to be retained in working memory (e.g. Bosch, Mecklinger & Friederici, 2001), in imagery tasks (e.g. Farah, Weisberg, Monheit, & Perronet, 1990), as well as in other delayed response tasks (Weber et al. 2005; Rösler, Borgstedt, & Sojka,1985, Gevins et al., 1996). Such deflections were associated with different functions, like decision making (Ruchkin, Munson, & Sutton, 1982, Johnson & Donchin, 1985), response selection (Falkenstein, Hohnsbein, & Hoormann, 1994), resources enabling operations in working memory (Rösler & Manzey, 1986) or completion of the first cognitive operation following target detection (Garcia-Larrea & Cezanne-Bert, 1998). However, to what extent similar positive deflections constitute a uniform phenomenon with specific functions is still under debate (e.g. Garcia-Larrea & Cezanne-Bert, 1998).
Distance differences, which were detectible in the positive posterior slow wave activity, were similar to those detected at centroparietal sites (P3b), where an increase in distance was associated with a decrease in amplitude. Similar to P3b and assuming that the ERP amplitude is proportional to a number of activated (or deactivated) units, these results seem to suggest that late encoding and / or retention mechanisms were stronger occupied if target distance decreased. If so, then the results would indicate that a decrease in sensory sensitivity can be compensated by an increase in resources allocation during stimulus evaluation / retention. However, this conclusion should be considered with caution, since the obtained distance effects may arise from differences in the intertrial latency variability across the distance conditions and / or from the temporal overlap of P3 and PSW components with CNV (see e.g. Rösler & Manzey, 1986)

Between 750 and 1000 ms, we obtained different topographical distributions of distance effects dependent on the delay condition ("1000" and "5000"). While delay "1000" condition

[25] Because the task was quite simple, we propose that operations, which may require a reallocation of attentional resources like proposed for high memory load conditions, were hardly involved and/or were similar in all eight distance conditions.

was associated with strong distance differences mainly localized over parietooccipital and anterior frontal areas, the longest delay condition exhibited much smaller effects at left inferior frontal and central locations. Although significant ERP differences over frontal areas were obtained in both delay conditions, their topographies and mean amplitude distributions across eight target conditions were quite different, suggesting specific delay dependent neuronal mechanisms. Moreover, posterior effects in the "1000ms" condition were similar to those obtained in the previous time window, where an increase in distance was accompanied by a decrease in positive activity, which was referred to as PSW. Apart from one electrode location, no significant effects at posterior sites were found, when a response was required after 5 seconds. These results seem to indicate that retention mechanisms of the same physical stimulus can change depending on the time of response.

Analyzing the nature of encoding processes in a series of studies, Fabiani and colleagues (for review see Donchin & Fabiani, 1991, Fabiani et al., 2000, Rugg, 1995) related the modulation of late positivities in memory tasks (labeled as P300) to mnemonic rather than to elaborative strategies (for similar hypothesis see also Bosch et al., 2001, suggesting the role of posterior positive waves primarily in perceptual aspects of working memory, like retention of image-like representations). Other results indicating a direct relation of posterior positive slow wave activity to perceptual difficulty seem to confirm this hypothesis (e.g. Ruchkin, Johnson, Mahaffey, & Sutton, 1988 and other studies cited there).

According to these findings, these results may indicate a change of processing characteristics from a rather "mnemonic" mode, which was prolonged in the "1000" ms condition, to a rather elaborative processing during the longest delay condition. However, since exact physiological as well as functional correlates of positive waves are still widely unknown, this conclusion remains very speculative.

It is worth mentioning that during the "5000" ms condition, posterior positive slow waves reached their peak about 600 – 700 ms and seemed to decay until about 1 second after that, indicating possible temporal range of a process reflected by this activity.

In summary, stimulus onset was followed by a group of phasic deflections, which tended to increase with an increase in target distance. We attributed these differences to different efficiency of detection and early encoding mechanisms associated with target eccentricity. A series of positive deflections following the early phasic activity showed an inverse relation to the target distance, suggesting stronger involvement of resources with a decrease in distance on this level of processing. Such differences were still present between 750ms and the "go

signal” under the “1000” ms condition, but were absent under the “5000” ms condition in a comparable time window. We speculate that this fact may reflect a switch from a rather mnemonic to a rather elaborative processing mode during the “5000” ms condition. Some other effects were obtained during the retention phase, which we could not attribute to specific components or functions due to the lack of comparable results and, thus, were not discussed.

4.3.2.3 Motor preparation

Figure 4-9 shows the rather different ERP dynamics at posterior recording sites, leading us to consider each delay condition separately.

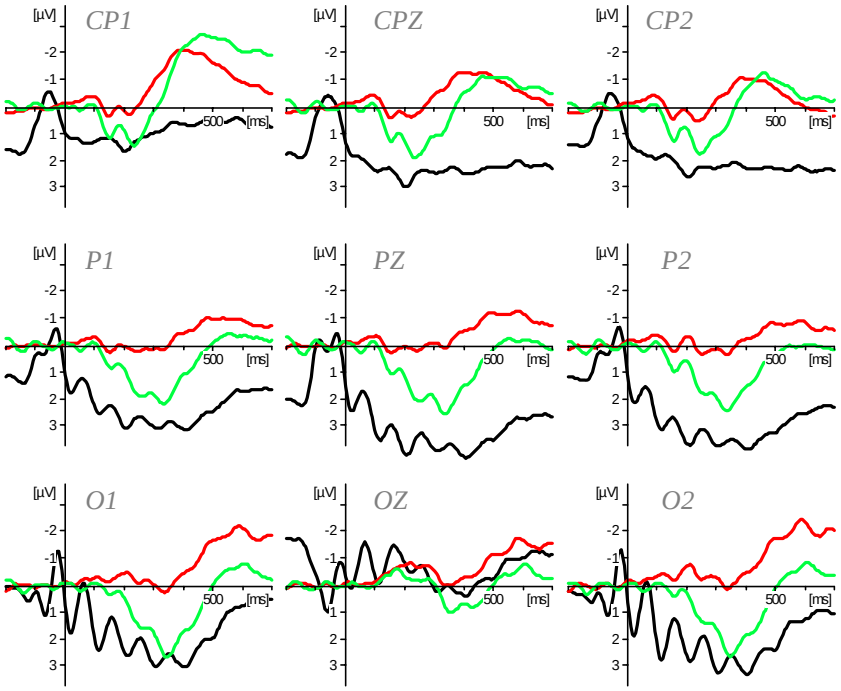


Figure 4-9. ERPs of three delay conditions (black = “200”, red = “1000”, green = “5000”) during motor preparation phase at selected posterior electrodes.

The ERPs of the shortest delay condition were characterized by pronounced phasic deflections (see also 4.3.2.1), which were accompanied by positive going waves. In contrast, during the “1000” ms condition neither rhythmic activity no transient positivities were obtained. Instead, biphasic ERPs over ventral occipital regions were detectible (see also Figures 4-2, 4-3 and 4-10). Moreover, the longest delay condition (“5000”) was associated with positive deflections over posterior regions lasting approximately until the movement onset, which seem to be entirely absent in the “1000” ms condition.

The results of the “time window specific” ANOVAs performed in the motor preparation phase are shown in Table 4-6.

Table 4-6: “electrode” x “distance” interactions of the motor preparation phase. Note: ANOVAs were performed for each delay condition separately; all tests were adjusted according to the method suggested by Huynh and Feldt; depicted degrees of freedom are not corrected, while probabilities represent corrected values; * p(F) <.05, ** p (F) < .01.

	“delay 200”			“delay 1000”			“delay 5000”		
	df	F	P	df	F	P	df	F	P
0-100	420, 8400	1.25	.187	420, 8400	.75	.803	420, 8400	.70	.852
100-200	420, 8400	**1.66***	**.025**	420, 8400	.83	.700	420, 8400	.89	.606
200-300	420, 8400	1.49	.072	420, 8400	1.16	.278	420, 8400	1.26	.181
300-400	420, 8400	**2.08****	**.003**	420, 8400	**1.53***	**.045**	**420, 8400**	**1.94****	.006
400-500	420, 8400	**3.00****	**<.001**	420, 8400	**1.90***	**.012**	**420, 8400**	**2.56****	<.001

During the shortest delay condition (“200”), different stimulus distances produced significant ERP changes in three of the five time windows. Moreover, in the time range between 200 and 300 ms after the “GO signal” a trend towards a significant “electrode” x “distance” interaction was detectible. However, it did not reach the significance threshold. The ERP amplitude during two other delay conditions was influenced only in the late period of the current phase by distance manipulation (300-400ms and 400-500ms time windows).

The detected distance differences over central regions were in all delay conditions comparable, and consisted of the amplitude modulation of a negative deflection preceding movement onset (see Figure 4-10). The longer the stimulus distance was, which had to be covered by the hand, the higher the amplitude of the mentioned potential was. However, during the delay “200” condition, ERPs of the eight target distances differed significantly already between 100 and 200 ms after the disappearance of the fixation light over central regions.

Moreover, the distance manipulation led to distance specific ERPs modulations at occipital electrodes only during the delay “200” and “1000” conditions. However, the ERP dynamics as well as the differences of distances were not comparable between these two delays (see Figure 4-9 for ERP courses and Figure 4-10 for distance differences at locations with maximal F values).

In contrast, during the longest delay condition (“5000”), significant distance differences were only detectible over centroparietal regions, additionally to the amplitude changes of the central negative deflection described above. This effect consisted of the amplitude decrease of a positive wave when distance increased (see Figure 4-10).

Although the effects found, except for frontocentral differences, were quite small, a “distance x delay x electrode” interaction reached the significance threshold in the time window between 400 and 500 ms in this processing phase, when all delay conditions were included in the statistical analysis (F = 1.41; P = .039).

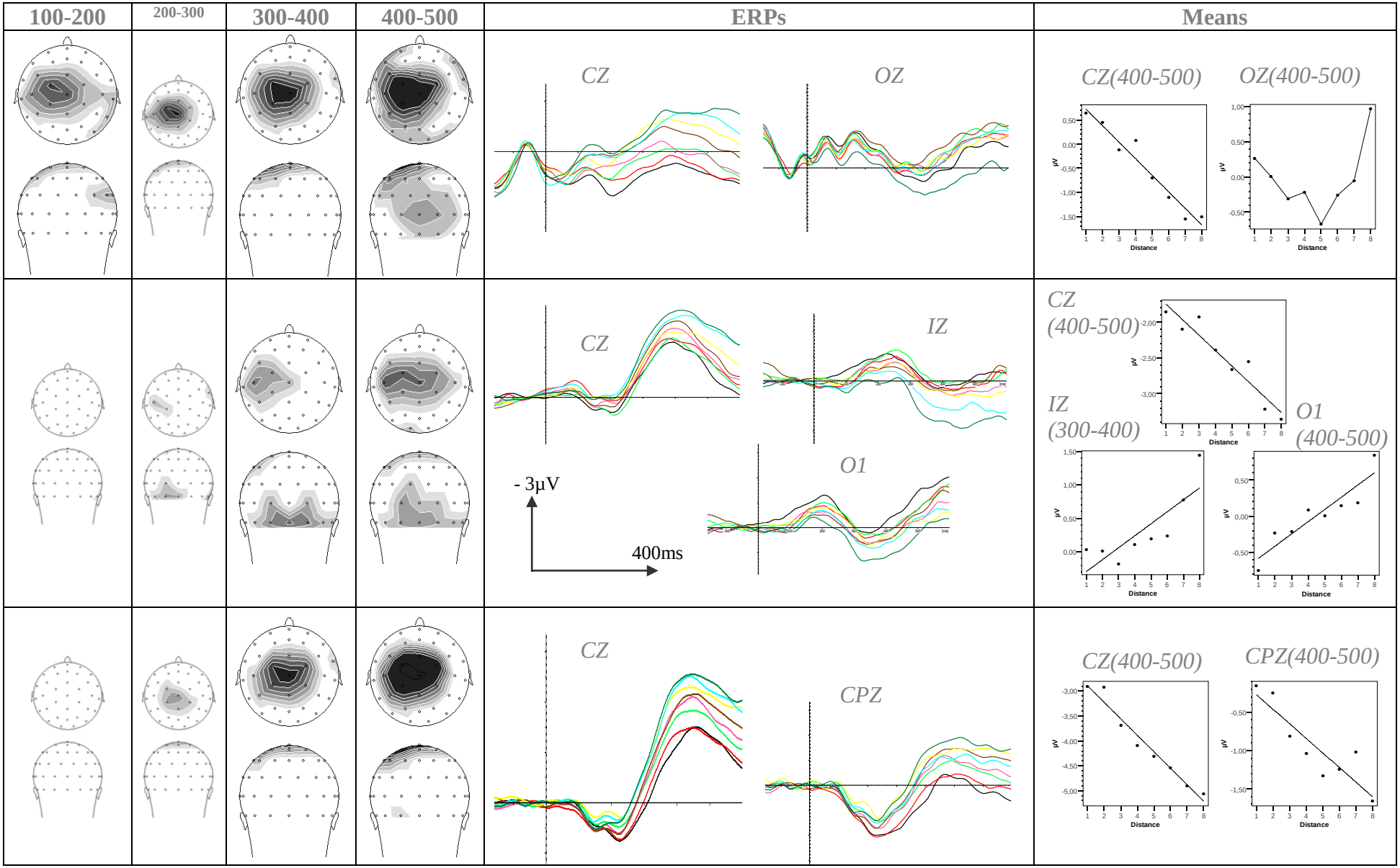

100-200
200-300
300-400
400-500
ERPs
Means
CZ
OZ
CZ(400-500)
OZ(400-500)
Distance
CZ
IZ
- 3µV
400ms
O1
CZ (400-500)
IZ (300-400)
O1 (400-500)
CZ
CPZ
CZ(400-500)
CPZ(400-500)

Figure 4-10: *Left:* topographical distributions of F values of factor "distance", derived from "electrode specific" ANOAVs computed for each delay condition separately (0 8); *Middle:* ERPs at selected locations (low-pass filtered signals (5Hz) are shown); *Right:* mean amplitudes of eight target conditions at selected electrodes in relevant time windows. The rows reflect the three delay conditions (from top to bottom): "delay 200", "delay 1000", "delay 5000".

Discussion

After the imperative "Go signal", we obtained similar distance differences at frontocentral electrodes for all delay conditions. Such deflections were often obtained prior to self-initiated voluntary movements and are often termed as "movement-related potentials" (MRP). By asking subjects to press a button at intervals of their own choice, Kornhuber and Deecke (1965) detected a slowly increasing negative shift at precentral electrodes preceding the motor response. This negative deflection, labeled as "readiness potential" or "Bereitschaftspotential" was extensively studied in similar recording situations and several components of MRP have been described (for review see Brunia, 1987, Brunia & Van Boxtel, 2000). A first premovement negative shift (labeled as "readiness potential 1", or "RP1") typically shows symmetrical distribution over central and parietal areas and was associated with motor presetting or preparation processes. A second negative potential is assumed to reflect context dependent parameter setting (or response selection mechanisms) and to be expressed in an asymmetric part of readiness potential ("RP2"). The last premovement negative deflection is the "motor potential" (MP), which is assumed to represent the command to move.

Although the voluntary movement paradigm is not directly comparable with the design used in the present study, there is some evidence that similar deflections to those described above are also present in externally cued arm movement, if subjects can predict the time point of the cue (Jankelowitz & Colebatch, 2002).

MRP components were shown to be sensitive to the manipulations of kinetic and kinematic variables. Slobounov et al. (1999) reported an amplitude increase in a late component of MRP (-100 to 0) in response to an increase in inertial load applied to finger movements (similar results were previously reported by Kristeva et al. 1990). In a further study of the same research group (Slobounov et al., 2000), a gradual increase in amplitude in the same time range was observed as the amplitude of motion increased. Other movement variables, like movement speed (Cooper & McCallum, 1989) or rate of force development (Slobounov et al., 1998) have also been shown to affect the amplitude of the cortical potentials preceding the response. Our results are in accordance with these findings and indicate that later stages of response preparation are highly dependent on kinematic and / or kinetic parameters of following movements and may reflect distance specific scaling of movement command (e.g.

scaling of neural input to the alpha motor neuron pool, see Gottlieb et al., 1989, see also "General discussion").

While this late processing stage of motor planning seems to be comparable during all delay conditions, other distance differences, found at different locations dependent on delay duration, indicate that processes taking place shortly before movement onset are not the same. As mentioned above, all delay conditions were associated with distance specific alpha activity, which was obtained over early visual areas in the time range between approximately 100 and 500 ms after stimulus onset. Thus, under the shortest delay condition the evoked alpha activity was present during the motor planning phase. According to the literature, we attributed this activity to the "iconic memory" mechanisms. Additionally, we found another effect over occipital areas in this delay condition, consisting of a distance specific modulation of a positive wave. Occipital electrodes were also affected by the distance manipulation during the delay 1000 condition. Although the topography of differences showed a more posterior distribution and the ERP dynamics of both delay conditions were quite different. Besides, motor planning processes associated with a delay of 5 seconds were characterized by additional deflections at posterior recording sites that were also sensitive to the distance manipulation. Similar results were reported by Reinvang et al. (1998, see also Magnussen, 2000). By varying the interstimulus interval (1 vs.10sec.) in delayed spatial frequency discrimination, the authors obtained a parietal component[26] in response to a test stimulus only during the 10 seconds condition. This positive deflection was attributed to memory retrieval as opposite to negative waves occurring in both delay conditions, which were referred to perceptual recall.

Thus, our results seem to suggest that motor planning processes including specific information of the memory trace are provided by a different electrophysiological substrate dependent on the delay duration. During the shortest and middle delay conditions, distance specific activity over early visual areas was obtained suggesting an involvement of early sensory information about the target distance in trajectory formation. However, different dynamics of differences and different topographic distributions of effects indicate mechanisms which differ between both conditions. Furthermore, during the longest delay condition no distance effects over occipital regions were found in this processing phase. Instead, a positive deflection over parietal cortex was shown to be sensitive to the distance manipulation. This fact may indicate an additional process (e.g. retrieval from short-term memory) which seems to involve other brain mechanisms.

[26] Component identification based on a source analysis procedure in this study.

4.3.2.4 Motor control

Table 4-7 illustrates the main results derived from windowed ANOVAs in the time range between movement onset and 500ms after it.

Table 4-7: Statistical results of "time window specific" ANOVAs performed on mean amplitude of respective time window with "distance", "delay" and "electrode" as factors. All tests were adjusted according to the method Huynh and Feldt (1976); the shown degrees of freedom are not corrected, while probabilities represent corrected values; * p(F) <.05, ** p (F) < .01.

Time windows	„electrode x delay“			„electrode x distance“			„delay x distance“			“electrode x delay x distance“		
	df	F	P	df	F	P	df	F	P	df	F	P
0-50	120, 2400	**4.78****	**<.001**	420, 8400	1.60	.052	14, 280	.91	.546	840, 16800	1,31	.088
50-100	120, 2400	**6.38****	**<.001**	420, 8400	**2.00****	**.002**	14, 280	1.17	.301	840, 16800	.93	.612
100-150	120, 2400	**5.41****	**<.001**	420, 8400	**2.82****	**<.001**	14, 280	1.32	.201	840, 16800	1.04	.395
150-200	120, 2400	**5.42****	**<.001**	420, 8400	**1.57***	**.047**	14, 280	1.31	.198	840, 16800	1.16	.216
200-250	120, 2400	**5.81****	**<.001**	420, 8400	**2.18****	**.004**	14, 280	.65	.824	840, 16800	1.04	.401
250-300	120, 2400	**6.46****	**<.001**	420, 8400	**2.73****	**<.001**	14, 280	.80	.664	840, 16800	.91	.649
300-350	120, 2400	**7.43****	**<.001**	420, 8400	**1.96***	**.018**	14, 280	1.15	.316	840, 16800	.91	.640
350-400	120, 2400	**7.10****	**<.001**	420, 8400	1.78	.050	14, 280	.76	.710	840, 16800	.90	.672

In all of the selected time windows the "delay x electrode" interactions became significant and the distance manipulation affected the ERP amplitude in four of the six time segments as expressed in significant "electrode x distance" interactions. Moreover, the last mentioned effects missed the significance threshold in the two residual time windows only marginally (see Table 4-7, time windows 0-50 and 350-400ms). Neither significant "delay x distance" nor "delay x distance x electrode" interactions were found, suggesting that the observed delay differences were independent from the distance effects.

The results of the "electrode specific" ANOVAs are depicted in Figure 4-11 (top). Significant differences between movements of different length occurred at first at over left centroparietal and frontopolar sites (50-150ms) and drifted then towards the frontocentral sites, showing again higher F values over the left hemisphere (200-400ms). Centroparietal differences were characterized as an increase in negative activity when movement distance increased. Near distances caused more negative activity at anterior frontal electrodes in contrast to far locations. Maximal F values of motor control phase were found between 250 and 300ms over left frontocentral areas. These effects were caused by a distance specific modulation of a negative deflection, which occurred from about 120 ms after movement onset and showed an amplitude increase with an increase in movement distance. Additionally, significant distance differences were found over occipital and occipitoparietal areas in the range between 250 and 300ms. Apart from the shortest target condition, an approximately linear decrease in negative activity was present when movement distance increased.

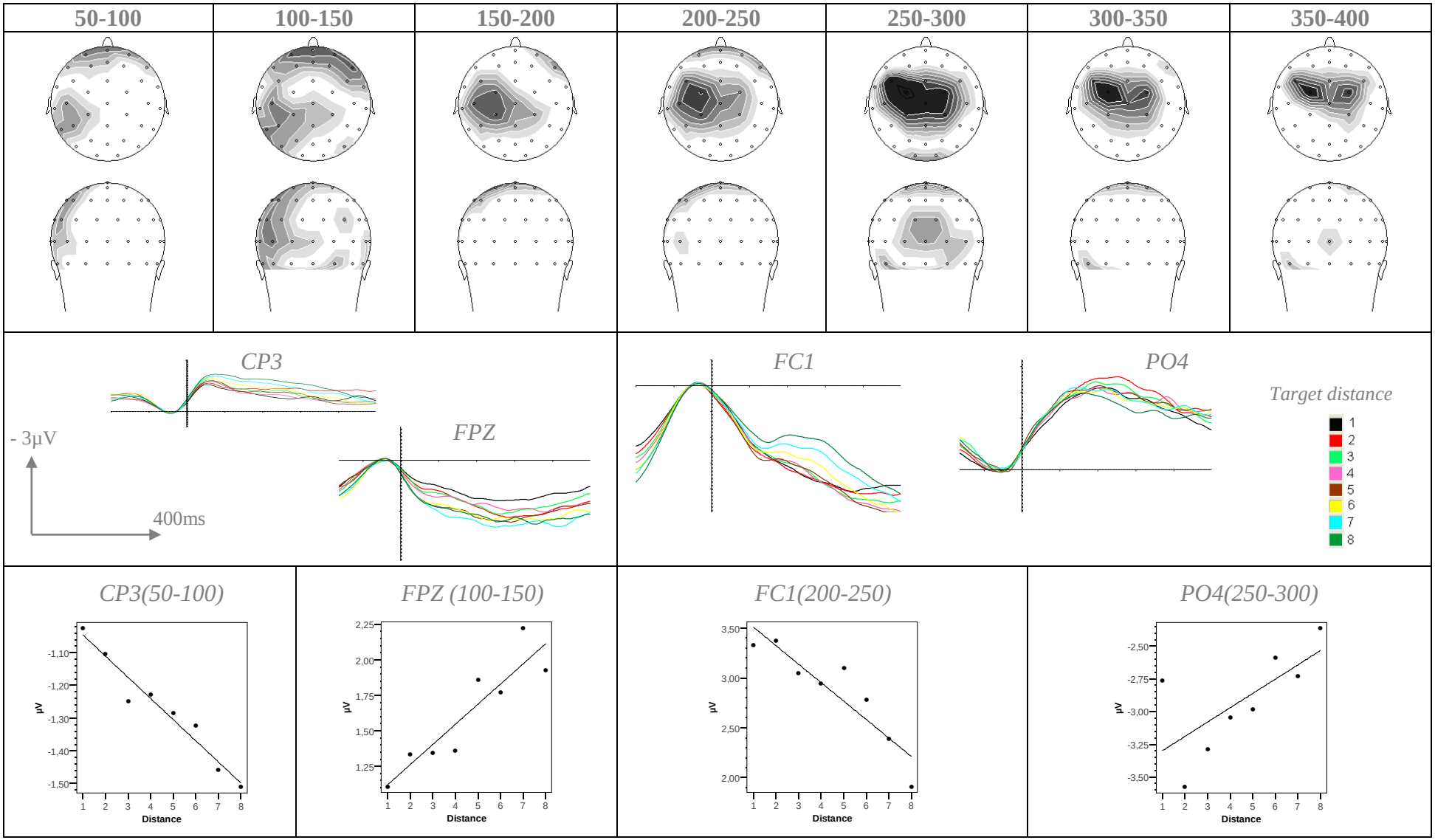

50-100
100-150
150-200
200-250
250-300
300-350
350-400
CP3
FPZ
FC1
PO4
- 3µV
400ms
Target distance
1
2
3
4
5
6
7
8
CP3(50-100)
FPZ (100-150)
FC1(200-250)
PO4(250-300)
µV
Distance

Figure 4-11: Top: F values of main effects “distance”, computed for each electrode including all delay conditions (0 [redacted] 9); Middle: ERPs at selected electrodes with high F scores (low pass filtered (5Hz) potentials are shown); Bottom: mean amplitude values of eight target conditions at selected electrode locations and in selected time windows.

Discussion and additional analyses

Figure 4-12 shows the temporal relation of measured kinematic parameters to distance specific brain responses.

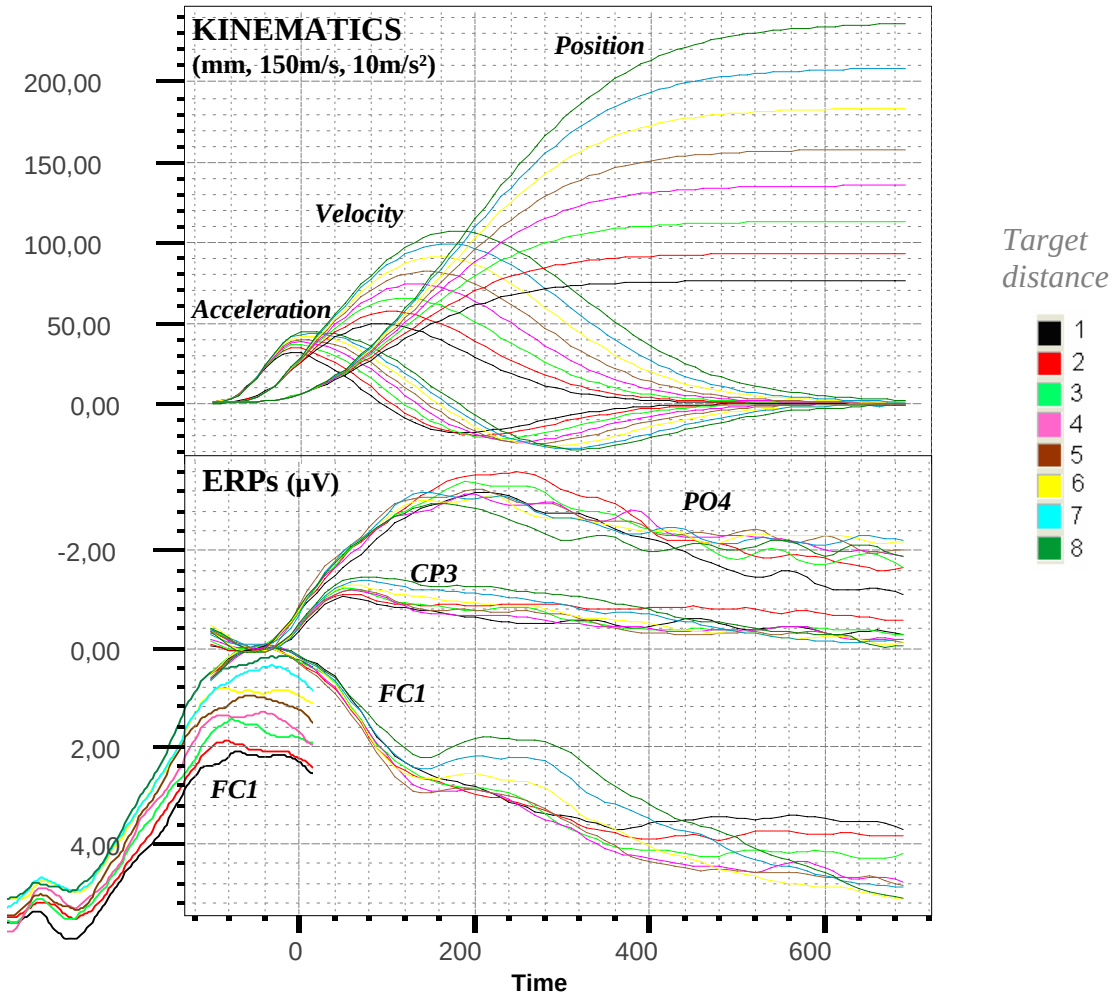


Figure 4-12. Kinematic parameters and ERPs, which showed significant distance differences during movement execution. Additionally, FC1 activity of motor preparation phase was also plotted to show largest distance effects preceding movement onset (time 0). Note: All ERPs were baseline corrected (-100/0) in respect to the beginning of the respective phase. Distance differences at frontopolar electrodes are not shown.

As in our previous study, where movements towards kinesthetic targets were investigated, the most pronounced distance differences occurred at the central and frontocentral electrode locations and were the result of a distance specific modulation of an ERP component that we referred to as N4, according to the literature (Brunia, 1987). This negative wave was obtained

in the time range of maximal deceleration (between 130 and 400 ms) and increased with an increase in movement distance. In contrast to previous findings suggesting primarily sensory feedback functions, we assumed, based on topography and a source analysis procedure, a rather executive or control mechanism associated with the modulation of the mentioned deflection. The results of the present study seem to support this notion. Maximal distance differences in the mentioned time range were found over left frontocentral areas, suggesting primarily involvement of motor areas in generating this deflection.

Moreover, we estimated the current source density of the first 400 ms of movement potentials averaged over all distance and delay conditions by using LORETA[27] ("Low Resolution Tomography", Pascual-Marqui et al., 1994, Pascual-Marqui, 1999).

The corresponding results are shown in Figure 4-13.

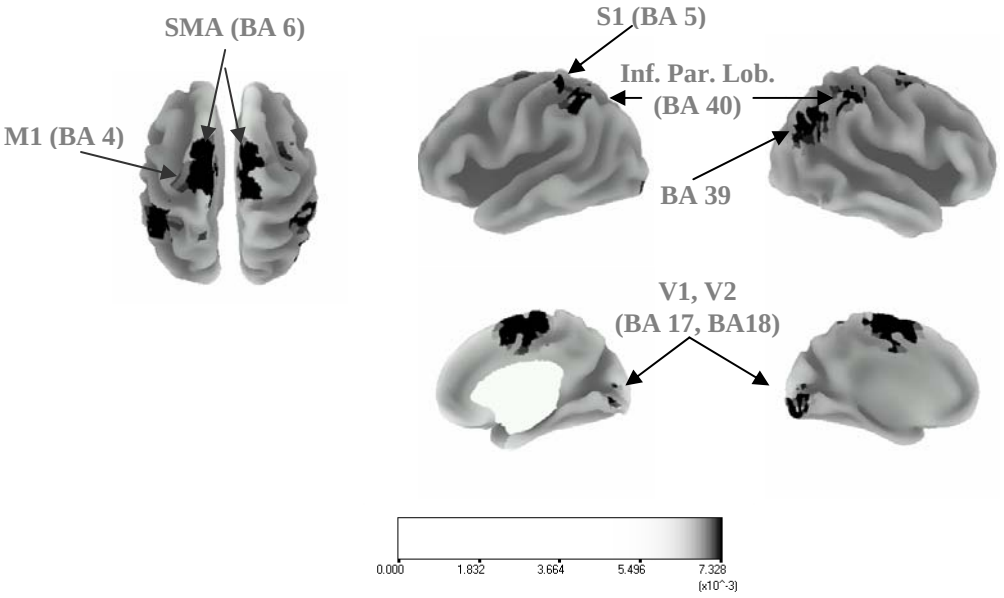


Figure 4-13. LORETA current density distribution estimated for the first 400 ms of movement control phase. Activity is color-coded, with maximum corresponding to black and zero to white.

The main cluster of activity comprised the SMA ("supplementary motor area") and left M1 ("primary motor cortex"). According to the statistical maps, in which distance differences were found rather over the left regions, the main source of N4 activity seems to be localized in M1. The large part of SMA activity may be a result of positive activity associated with the decay of "motor potential" obtained in the previous processing epoch.

[27] LORETA estimates intracerebral distribution of current density generating the scalp recorded ERPs. Starting from the physiological core assumption that neighboring neuronal sources are active synchronously and simultaneously, the LORETA algorithm solves the inverse problem by finding the "smoothest" of all possible activity distributions. The resulting solutions represent the amplitude of current density at each voxel in neuroanatomic Talairach space (μA-equivalent), which is restricted to gray matter and hippocampus.

Shortly after movement onset, we obtained further distance differences over left parietal and parietocentral areas. The activity of corresponding ERPs was characterized by a steep negative potential peaking at the time between maximal acceleration and maximal velocity values and by a slowly declining course afterwards. The current sources in the left hemisphere extended from S1 ("primary somatosensory cortex") to inferior parietal regions (BA 40). Our previous study revealed similar differences and sources, which we referred to possible sensory and / or internal feedback functions. The time range of the negative peak over left centroparietal areas (about 80 ms after movement onset[28]) and its possible neuronal origin (near the somatosensory cortex) may suggest the role of this component in proprioceptive feedback functions (physiological delays for proprioceptive signals are reported to be around 120 ms, see Jeannerod, 1988).

Between 250 and 300 ms after movement onset, differences across distance conditions were found over early visual areas. Interestingly, a trend towards an increase in activity with a decrease in distance was observed. The performed source analysis indicated an origin of activity in primary and secondary visual cortexes (V1, V2). Since no visual input during movement execution was present, visual activity obtained in the current study could reflect a "top down" process, possibly indicating an anticipated target position. Moreover, maximal negativity over visual areas was achieved in the time range (200ms), which is assumed to be critical for visual feedback mechanisms (e.g. Keele & Posner, 1968, but see below). Thus, a possible role of obtained visual activity may also consist of providing actual information about target position.

In order to get further insights into movement control mechanisms, we computed correlation coefficients between maximal acceleration values and the amplitude of movement end point position. Since early kinematic parameters (like peak acceleration) are assumed to be preplanned before movement to a large extent (e.g. Gordon & Ghez, 1987b), this analysis allow conclusions to be drawn about control processes taking place during movement execution. These results are depicted in Figure 4-14 and Table 4-8. As shown, mean correlation coefficients decreased with movement distance, indicating a decreasing influence of preprogrammed movement amplitude on the reproduced distance. This result may be related to an increasing relevance of on-line processes with movement distance, like of "compensatory adjustments" suggested by Gordon and Ghez (1987b, see also Messier and Kalaska, 1999), which are assumed to correct the initial movement trajectory depending on feedback signals (e.g. by the modulation of temporal control aspects like movement duration).

[28] Due to used markers for movement onsets (5mm threshold), the "real" time of peak in respect to the movement onset can be expected to be several milliseconds later.

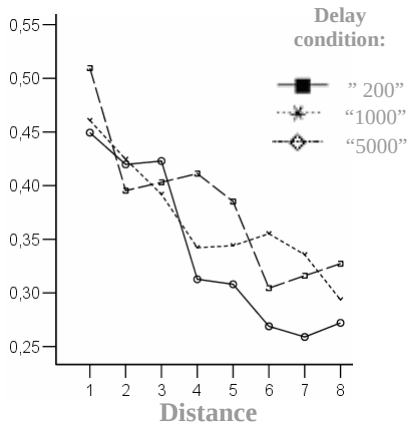


Figure 4-14. The averaged correlation coefficients of 24 experimental conditions for all subjects.

Table 4-8. Statistical results of ANOVA performed with correlation coefficients (see text). All tests were adjusted according to Huynh and Feldt (1976). *p<.05; **p<.01

Effect	df	F	P
"Delay"	2,40	,46	,601
"Distance"	7,140	**5,11****	**,002**
"Delay x Distance"	14,280	,66	,788

In summary, we obtained four main clusters of distance differences, which occurred during movement execution phase. Differences over the left centroparietal regions may be associated with proprioceptive feedback mechanisms, while modulation of visual activity may represent anticipatory and / or visual feedback processes. However, they may also reflect neuronal markers of internal feedback processes, which assumed to be involved in movement control (see e.g. Desmurget & Grafton, 2000 for a review). Moreover, according to a recent view of motor control processes, initial motor plan is only crudely specified before movement onset and has to be updated during movement execution (e.g. Desmurget and Grafton, 2000). The performed correlation analysis supported the view that the longer the movement distance was, the more corrective processes were involved. The modulation of the frontocentral deflection (N4) seems to be closely related to such corrective command components, since its topography and possible neuronal origin indicated a probable involvement of areas adjusting primary motor cortex. Furthermore, the temporal dynamic of N4 modulation suggests that the process begins about 130-150ms after movement onset in all distance conditions (see also our previous results). This fact may indicate a temporal threshold of reactivation of motor neurons and may reveal a possible explanation for the results of the correlation analysis. According to this, short movements are performed mainly in an open-loop manner because corrective mechanisms may be time dependent and can only occur after a certain interval. These conclusions seem to be in agreement with the results reported by Mills and Kimiskidis (1996). By using transcranial magnetic and electrical stimuli during ballistic forearm and finger movements, the authors identified two phases of cortical excitability, one at the beginning of movement and a second starting about 100 ms after movement onset. Moreover, based on their results, the authors attributed the second phase to a similar mechanism, described above (corrective command based on error signals).

4.4 General discussion

Encoding, retention and motor planning

The primary goal of the present study was to investigate the effect of time on visuomotor processes. By analyzing kinematics and errors of performed movements, we did not find substantial changes of these parameters, indicating that hand movements were controlled similarly under all delay conditions (see also below). However, significant distance specific and delay dependent differences in reaction times suggested that motor planning processes differed between at least the shortest and the two longer delay conditions.

Main ERP differences of the eight distance conditions during motor planning phase were obtained at central electrode locations in all delay conditions. We attributed them to the distance specific modulation of “motor potential” (see discussion and below). However, in addition to these effects, the analysis of event-related potentials during motor planning phase revealed not only quite different dynamics of three delay conditions, but also distance effects being localized at different electrode locations dependent on delay duration. These are strong indices for delay dependent changes of processes, which take place shortly before movement initiation.

The ERPs of the shortest delay condition were mainly characterized by rhythmic activity in alpha band over early visual areas, which were accompanied by positive deflections with similar topography. Both components were affected by the distance manipulation suggesting their role in stimulus specific processing. Since evoked alpha activity is assumed to represent an early sensory retention system operating on a low level of information processing (see 3.2.1), these results seem to suggest that parameter settings for an upcoming movement is based on such basal information processing in early visual areas (e.g. V1). Moreover, distance differences in respect to the mentioned positive component resembled the reaction times, which showed a u-shaped distribution across eight target location. This positive activity may reflect a process of reading out the relevant information provided by alpha activity.

The evoked activity under the“1000ms” condition during the motor planning phase was influenced by the distance manipulation also over central and occipital areas. However, the topography of distance differences as well as dynamics of posterior ERPs were not comparable to the shortest delay condition. It is worth mentioning that the voltage distribution in the first 300 ms after the “go signal” showed negative activity with a maximum over right occipital sites, while during late range of retention interval a positive maximum with nearly

the same location was obtained (see Figure 4-15, see also Figure3). Since positive slow waves are assumed to reflect decreased brain activity (e.g. Birbaumer et al., 1990), this observation may suggest that regions deactivated during retention would be reactivated during motor planning[29]. Additionally, according to several results indicating the role of posterior positive wave especially in perceptual or mnemonic processes (see 3.2.2), a decrease of cortical excitability may serve as neuronal substrate providing intermediate retention of information on a mnemonic / perceptual level.

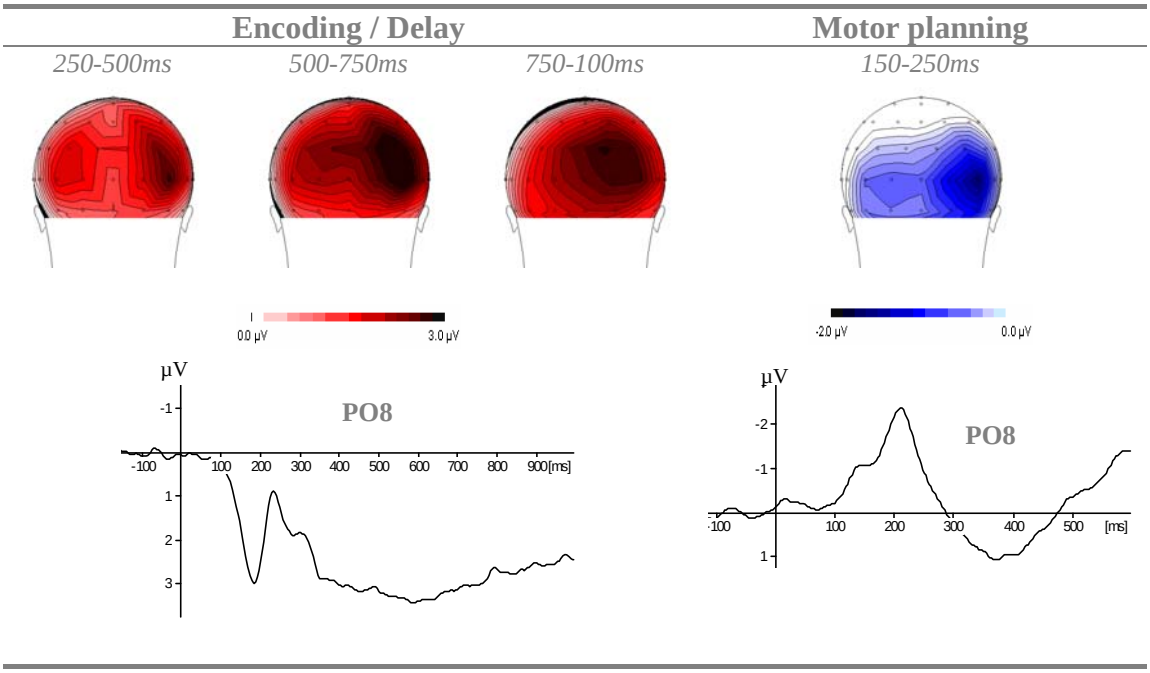


Figure 4-15. Selective results of encoding and motor planning phases during the "1000" ms condition. Mean voltage maps and ERPs represent activity averaged over eight distance conditions.

But these proposals should be considered with caution. The distance manipulation was associated with slightly different topographies of effects during the delay interval and the motor planning phase in this condition, making possible conclusions difficult. The visual data inspection also revealed visible distance differences in an early time range of the motor planning phase over mentioned electrodes. However, they did not reach the significance threshold as indicated by the statistical analyses. We assume that this fact may be a result of a rather poor signal to noise ratio and an overlapping of several deflections in this time range. Nonetheless, the results show that inhibitory distance specific mechanisms (i.e. transient

[29] According to Birbaumer at al. (1990) positive slow potentials may result in consequence of threshold regulation mechanisms of cortical excitability. Enhanced activity induced by a stimulus requires a compensatory reduction of excitability in order to prevent a chain reaction of neuronal excitation. Such inhibitory mechanisms are assumed to be reflected by transient positive shifts in the EEG. The functional role of similar waves in context of memory is considered by the authors as activity reduction in order to allow "reverberation" of relevant information in selected networks. But, inhibition is referred to as noninvolved networks by the authors.

positive shifts) are active during retention interval at posterior recording sites and that motor planning is associated with distance specific phasic activity at similar locations during the 1000 ms delay condition. This fact may reflect one specific mechanism of retention and recall of relevant information required for motor planning.
No such relation was observable during the “5000” ms condition. Distance differences at posterior electrodes disappeared already after 750 ms post stimulus during retention interval. In the range between 1000 and 5000 ms, we did not find any distance specific differences. Moreover, pronounced positive activity at posterior sites was decayed about one second after target presentation. Although the posterior activity during early planning phase was similar to the activity observed during the 1000 ms condition, no distance differences were found. Instead, eight distance conditions differed over centroparietal regions additionally to the MRP during motor planning phase indicating an additional process, which may be associated with information retrieval from short-term memory.
These results as a whole, suggest that the planning of goal directed movements may involve different electrophysiological and possibly functional mechanisms dependent on the time between stimulus and response.

On-line control of hand movements

By investigating kinematic and electrophysiological parameters during movement execution, we aimed to replicate our previous results and to provide further insights into the nature of movement control mechanisms.
Acceleration, velocity and position changes are extrinsic kinematic parameters, which are closely related to muscle activity visible in EMG (electromyogramm) recordings (Gordon & Ghez, 1984, Ghez & Gordon, 1987; Gordon & Ghez, 1987a; Brown & Cooke, 1990, Cooke & Brown, 1994, Gottlieb et al., 1989). In contrast to slow movements, which are characterized by continuous EMG activity, rapid joint displacements are produced by two phasic contractions of agonist muscle at the beginning and at the end of the movement (labelled AG1 and AG2), and an intermediate burst in the antagonist muscle (ANT) (for review see e.g. Berardelli et al., 1996). AG1 activation is assumed to provide the force to start the movement, which is decelerated by the following antagonist activity (ANT). The second phasic agonist response (AG2) is supposed to terminate the decelerative force pulse and, thus, to stabilize the limb at the end of movement. Some other findings suggested that the AG2 burst may also be

related to reafferent feedback mechanisms associated with adjustments of internal movement representations to actual information (MacKinnon & Rothwell, 2000).

There is some evidence that M1 (primary motor cortex) is essentially involved in generating these muscle responses (Sergio & Kalaska,1998, Sergio et al., 2005). By measuring neural activity in caudal parts of monkeys' primary motor cortex, these studies demonstrated that movement related signals of many cells (61%) corresponded to the muscle activity, as expressed in force profiles and the EMG signal.

Our results relating to the frontocentral component during movement execution seem to resemble these findings. The performed source analysis and topographies of distance differences suggested a possible origin of this signal in motor areas near M1. In our previous study as well as in the current experiment, the negative peak was obtained in the time range of maximal deceleration, indicating a possible role of this component in limb deceleration and / or in control of ANT burst. However, there is evidence that activity in the antagonist muscle is greatly reduced (or even disappear) in movements to mechanical stops (Berardelli et al., 1996). In our previous study, subjects performed hand movements, which were mechanically braked and had to reproduce the given location of the stop by a second movement. Both movement types showed similar N4 modulation (first movement type was even associated with greater activity and larger distance differences) indicating that ANT activity may not necessarily be coupled with N4 activity.

It was further suggested that patterns of muscle activity visible in EMG recordings and kinematic profiles are generated by two central command components, a "pulse" signal, which provides the driving force for setting the limb in motion[30], and a "step" component, which controls the terminal steady state force (e.g. Ghez & Vicario, 1978). This "pulse-step model" was initially used to describe eye movements (Robinson, 1973) and was later assigned to arm movements being integrated in many motor research fields (Ghez & Vicario, 1978, Ghez, 1979, Barto et al,1999, Gottlieb et al., 1989, Karniel & Inbar, 1999, Feldman & Levin, 1995, Suzuki & Yamazaki, 2005). Following this, one may assume that pronounced distance differences found shortly before movement initiation over central and frontocentral areas could be associated with different distance specific planning of "pulse" signal. Movements to far targets, which involve more muscle activity compared with movements to near targets, could be initiated by activation of larger parts of neural tissue within motor areas (i.e. require higher "pulse"). A second burst of activity over frontocentral regions during movement

[30] E.g. neural input to the alpha motor neuron pool, see Gottlieb et al. (1989).

execution (N4) could be further referred to the mentioned “step” command, which possibly controls AG2 activity.

However, our results allow only restricted statements about exact functions of these deflections and have to be validated by further studies. A decrease in correlations between peak acceleration and the amplitude of the end position with target distance may indicate a possible functional aspect of N4 modulation. According to the classical theory of motor control, reaching movements contain two components: a ballistic phase that is controlled by a crude preprogrammed motor plane, and a late adjustment phase that is dependent on feedback mechanisms (e.g. Desmurget & Grafton, 2000). Our correlation analysis indicated that the implemented distance manipulation was associated with changes of relation between preprogrammed and on-line control mechanisms.

Moreover, the obtained modulation of N4 component occurred in a late phase of movements and was associated with the largest distance differences obtained in this processing phase. Thus, our results seem to suggest that N4 activity is essentially involved in corrective processes during the movement adjustment phase.

4.5 Summary and Conclusions

In the present study we investigated the effect of varying delay duration on planning and execution of linear hand movements towards visual targets. By varying target eccentricity we manipulated the content of the memory trace and pursued the distance differences observable in ERPs from target onset to the movement execution. As a result of this we detected different delay dependent distance effects during motor planning phase and attributed them to changes in access to initially the same information. Due to lack of comparable studies, only restricted statements about functional and regional properties of identified phenomenon were possible. Nevertheless, the current results seem to be compatible with the idea of "temporal markers", mentioned in the introduction. According to this, initial visual information is passed through several, temporally and functionally separable, representation formats (e.g. early sensory store, perceptual on-line system, and short-term / working memory) and can be used on all of these hierarchical levels for motor planning, dependent on task requirements (e.g. time). Interestingly, the sequential model of visuomotor transformation processes mentioned in the introduction (Flanders, Tillery, & Soechting, 1992) was based on a series of psychophysical studies in which delay intervals between 3 and 5 seconds were implemented. By using delay conditions of 3 and 30 seconds Chiffie et al. (1999) also argued for planning in body coordinates, emphasizing rather a hand-centered representation (as opposite to shoulder-centered planning proposed by Flanders, Tillery and Soechting, 1992). In contrast, single cell recording results reported by Buneo et al. (2002), which were interpreted as evidence for direct planning in eye-centered coordinates, stemmed from experiments with delays of 600 – 1000ms. Moreover, a "conversion on demand model" suggesting retention of target information used for motor planning in eye coordinates was based again on short delay conditions (Henriques et al., 1998).
Thus, considering a high diversity of empirically shown and theoretically possible sensorimotor coupling mechanisms, the time aspect may play a critical role in the involvement of a certain process.

Moreover, it was possible to replicate the main results from our previous study in respect to the electrophysiological markers of motor control processes. We obtained a distance specific modulation of an ERP component, which seems to play an important role in movement execution. According to our working hypotheses, this deflection may essentially be involved in trajectory adjustments based on internal and / or sensory feedback signals.

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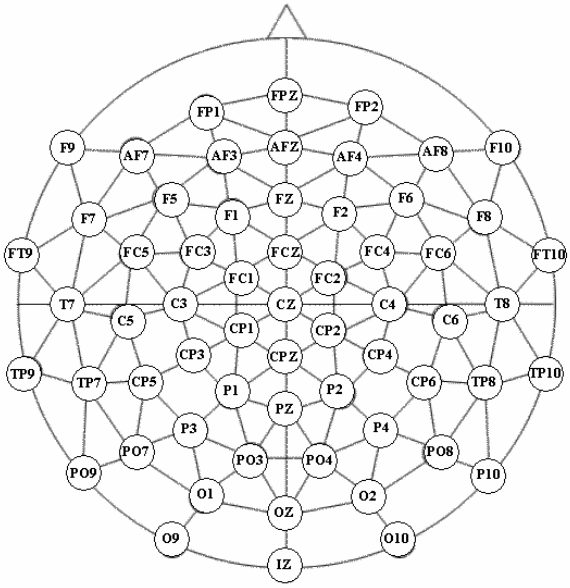
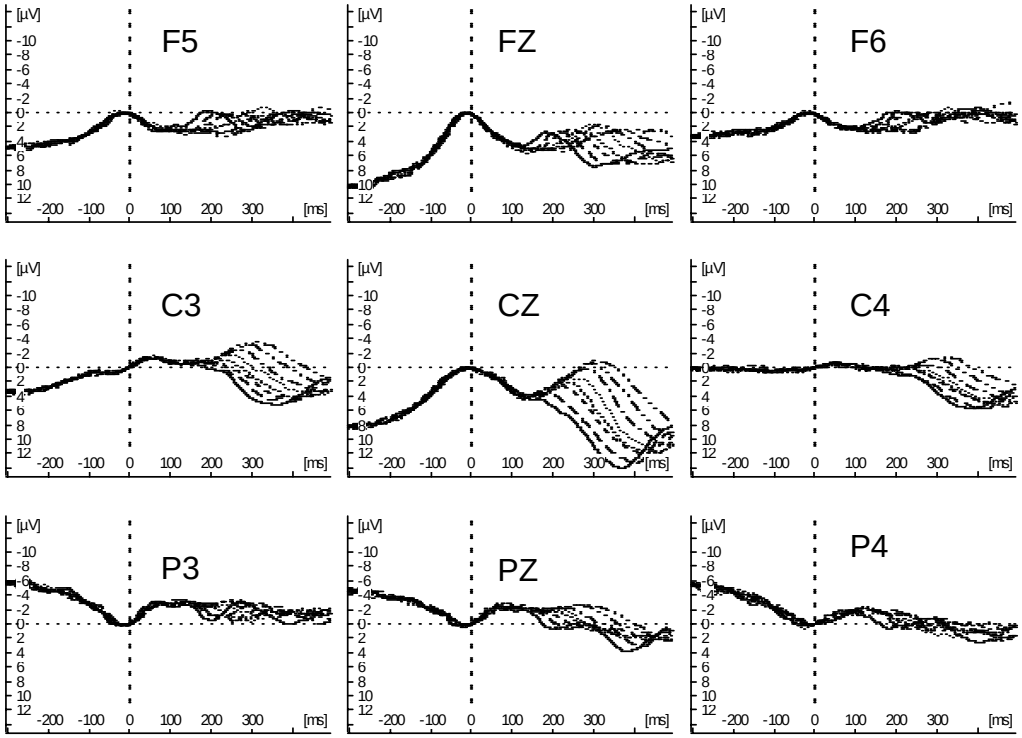
6 Appendix

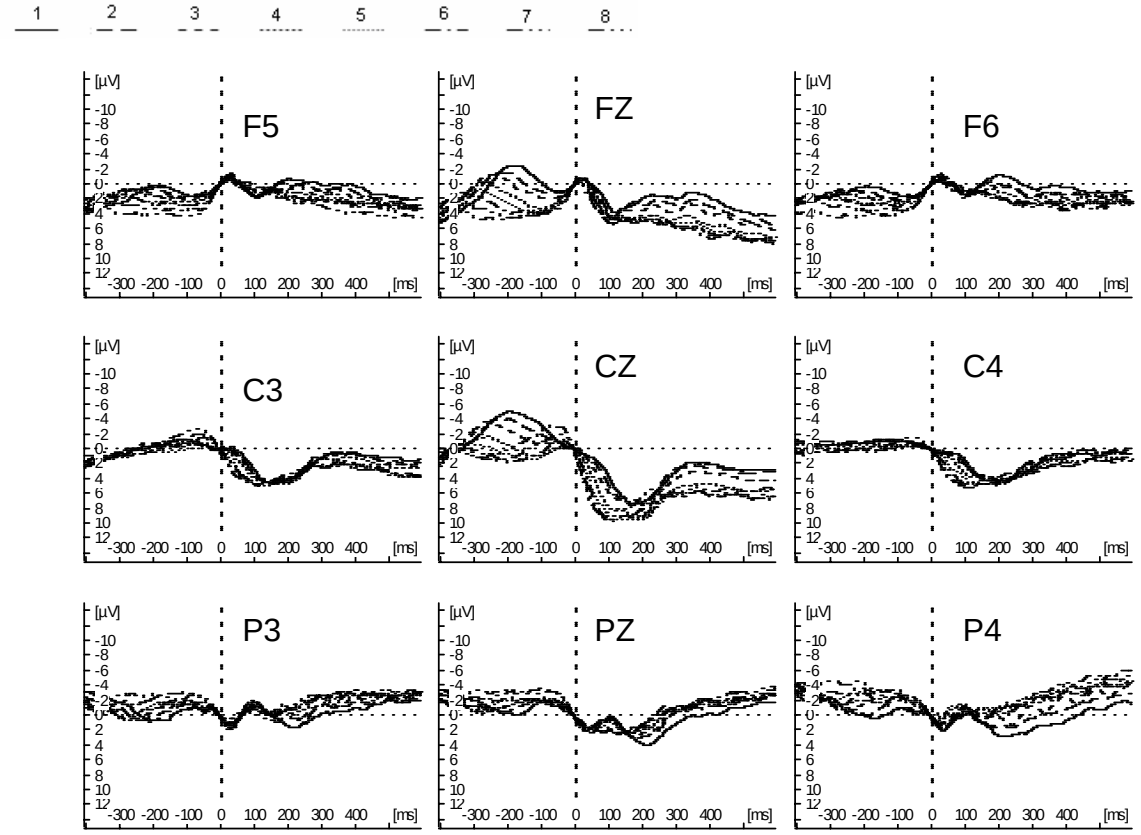
Appendix 3-A. Layout of the electrode array used in both EEG-Studies.



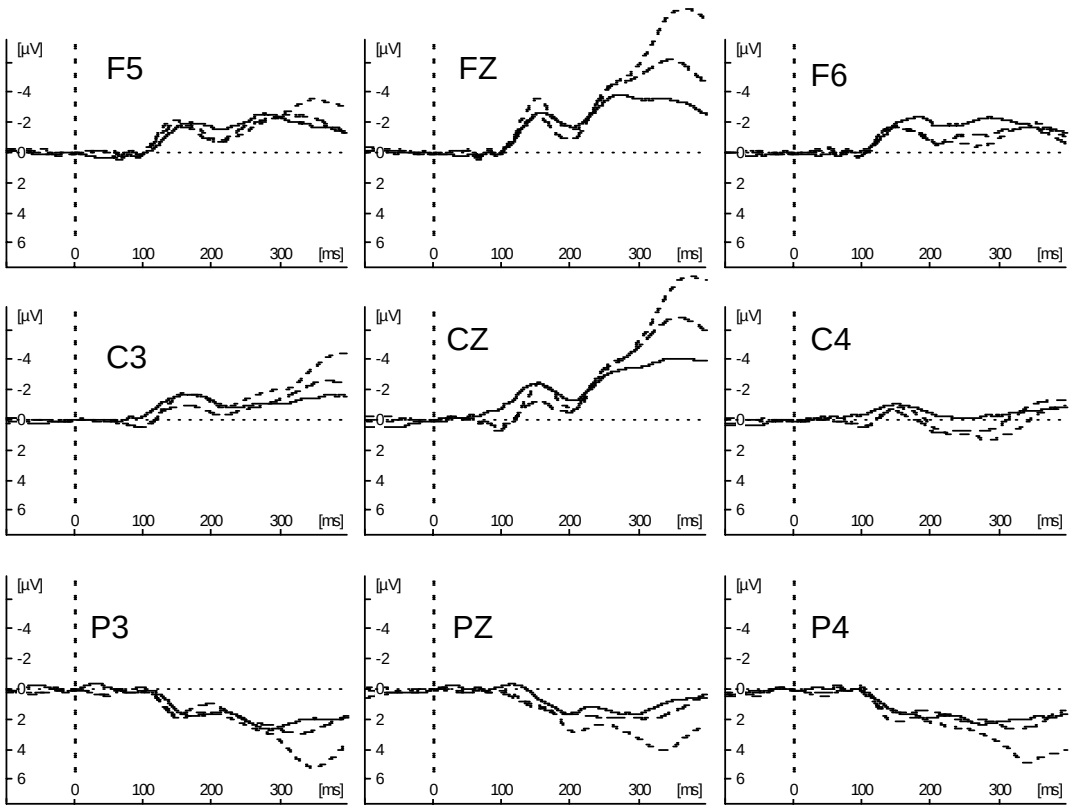
Appendix 3-B. *EEG-Study 1*: ERPs of the locating movement phase; each line represent a target location averaged over all delay conditions with follow line assignment:
1 2 3 4 5 6 7 8. The time scale is adjusted to the onset of movements.



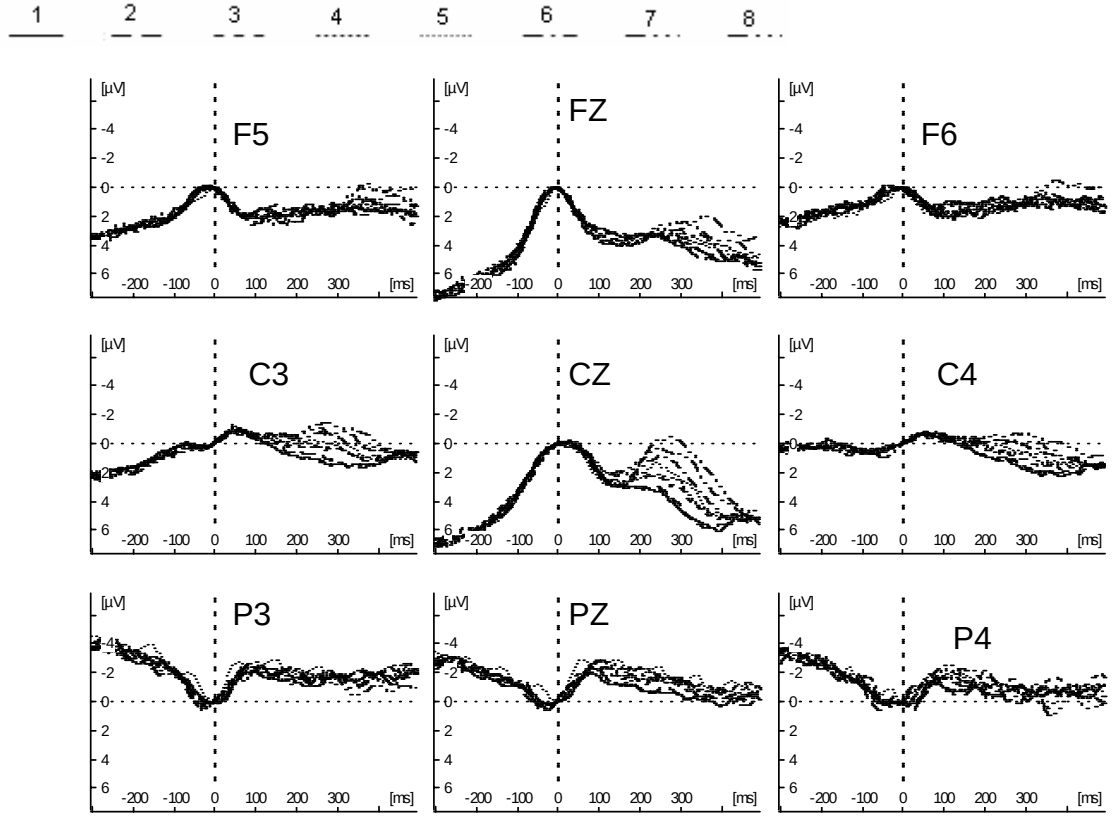
Appendix 3-C. *EEG-Study 1:* Over all delay conditions averaged ERPs of 8 distance conditions around the time point of the stop (represented by vertical dashed line);



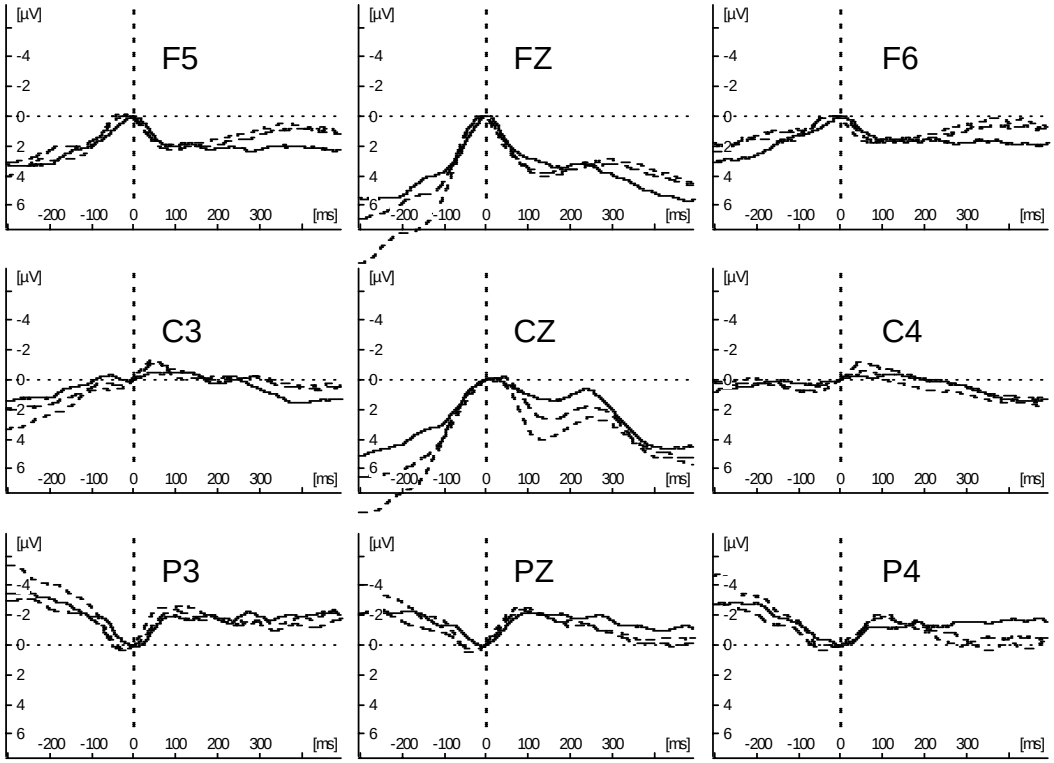
Appendix 3-D. *EEG-Study 1:* ERPs of three delay conditions during MP phase; —— delay "0", - - - delay "1", ... delay "5". ERPs are synchronized to the latency of the imperative "go-signal".



Appendix 3-E. *EEG-Study1*: ERPs of each distance condition during reproduction phase (vertical dashed line reflects movement onset); type of line represents target locations in ascending order:



Appendix 3-F. *EEG-Study 1:* Evoked activity of three delay conditions during reproduction; —— delay "0", - - - delay "1", ... delay "5".



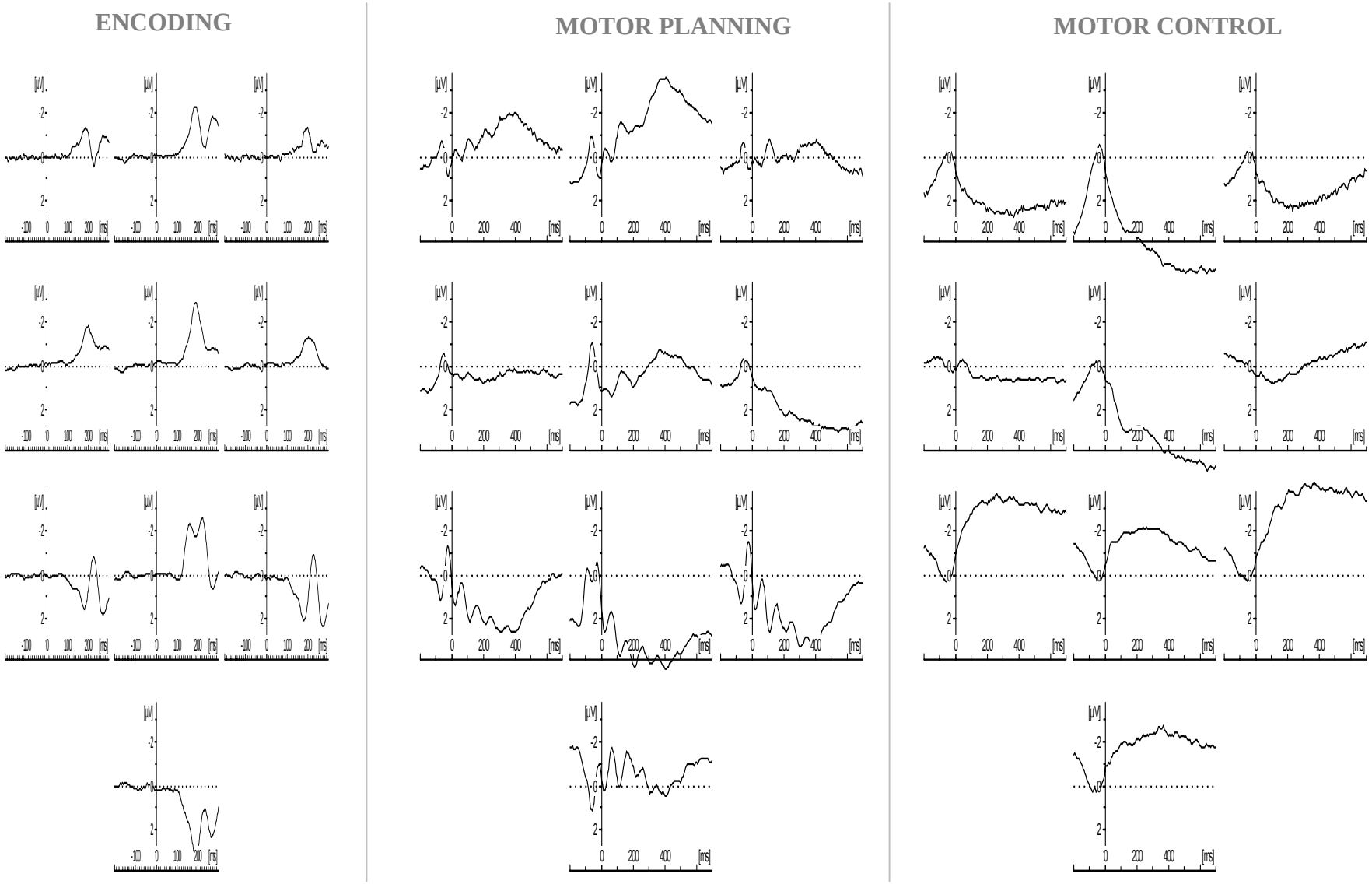
Appendix 3-G. *EEG-Study 1:* "Delay x Distance " (DLxDS) and "Electrode x Delay x Distance" (ElxDlxDS) interactions of time window specific ANOVAs; LM = locating phase, RM = reproduction movement, S = processing after the stop, MP = motor programming, D = delay phase. Note: all tests were adjusted according to the Greenhouse-Geisser method.

		Measurement Interval											
		0-50ms		*50-100ms*		*100-150ms*		*150-200ms*		*200-250ms*		*250-300ms*	
Phase	*Interaction*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
LM	*DLxDS*	1.2	.304	0.5	.849	1.2	.287	1.2	.334	1.5	.193	0.7	.648
	ElxDLxDs	1.1	.401	1.0	.476	1.2	.254	1.2	.320	1.3	.225	1.2	.311
RM	*DLxDS*	1.4	.225	1.5	.176	1.6	.152	1.2	.289	1.4	.205	1.5	.165
	ElxDLxDs	1.1	.372	1.2	.301	1.0	.478	1.1	.398	1.1	.377	1.1	.353
S	*DLxDS*	0.4	.898	1.3	.243	0.6	.769	1.1	.348	0.4	.917	1.5	.154
	ElxDLxDs	1.3	.220	1.4	.151	1.1	.376	1.2	.324	1.2	.287	1.3	.253

		100-150ms		*150-200ms*		*200-250ms*		*250-300ms*		*300-350ms*		*350-400ms*	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
MP	*DLxDS*	0.9	.515	1.1	.358	1.0	.436	1.1	.399	0.7	.643	1.0	.416
	ElxDLxDs	1.1	.339	1.1	.397	1.0	.430	1.1	.365	1.0	.439	1.1	.347

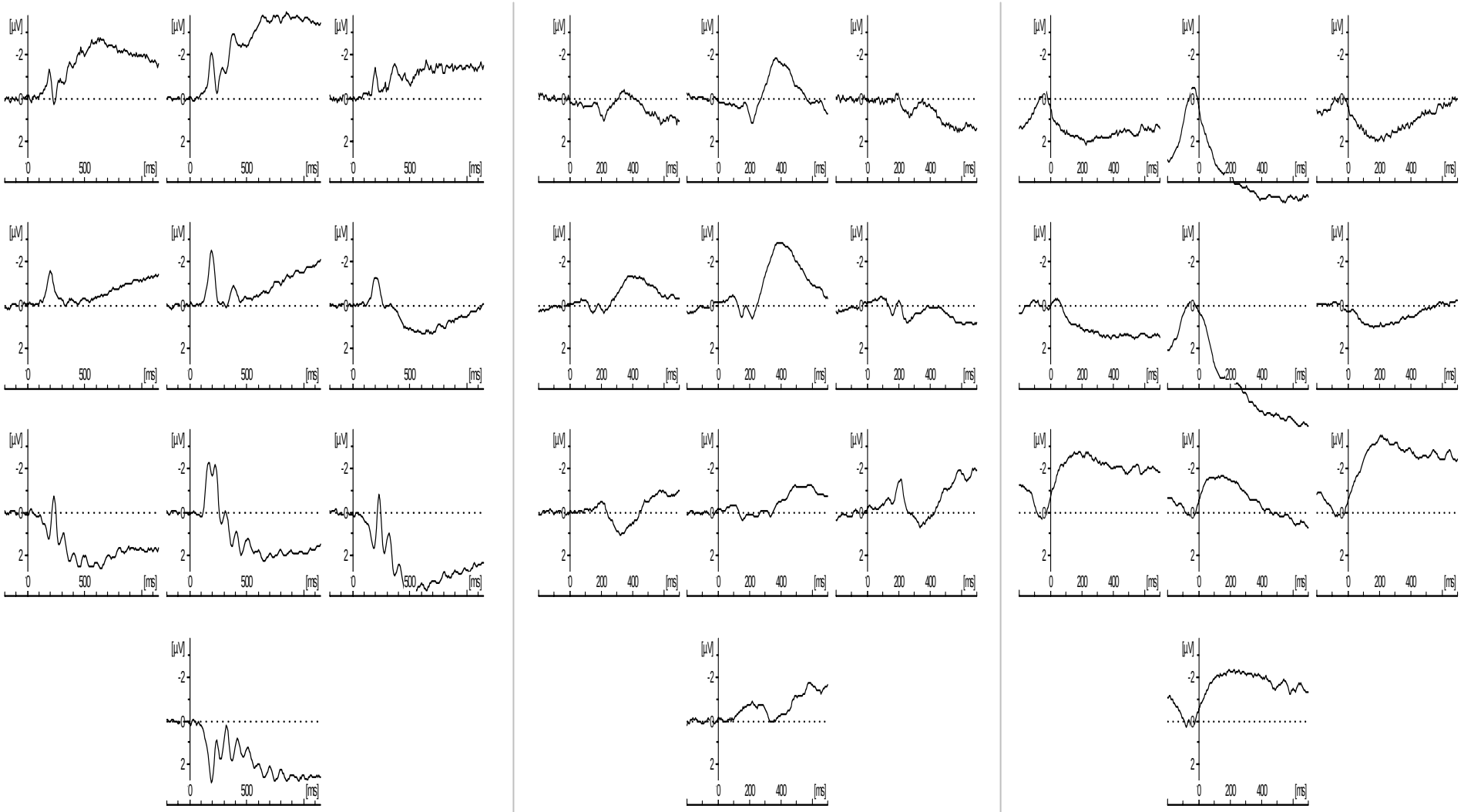
		Time range I		*Time range II*		*Time range III*	
		F	*P*	*F*	*P*	*F*	*P*
D	*DLxDS*	0.5	.830	1.4	.207	1.8	.093
	ElxDLxDs	1.2	.264	1.3	.228	1.3	.216

Appendix 4-A. *EEG-Study 2:* ERPs at F5, FZ, F7 (upper array), C3,CZ,C4 (second array), P3, PZ, P4 (third array) and OZ (bottom array) during the defined processing phases in the short delay condition ("200"). Note: all ERPs are adjusted to the respective trigger and are baseline corrected in respect to the time range of –100-0 preceding each phase.

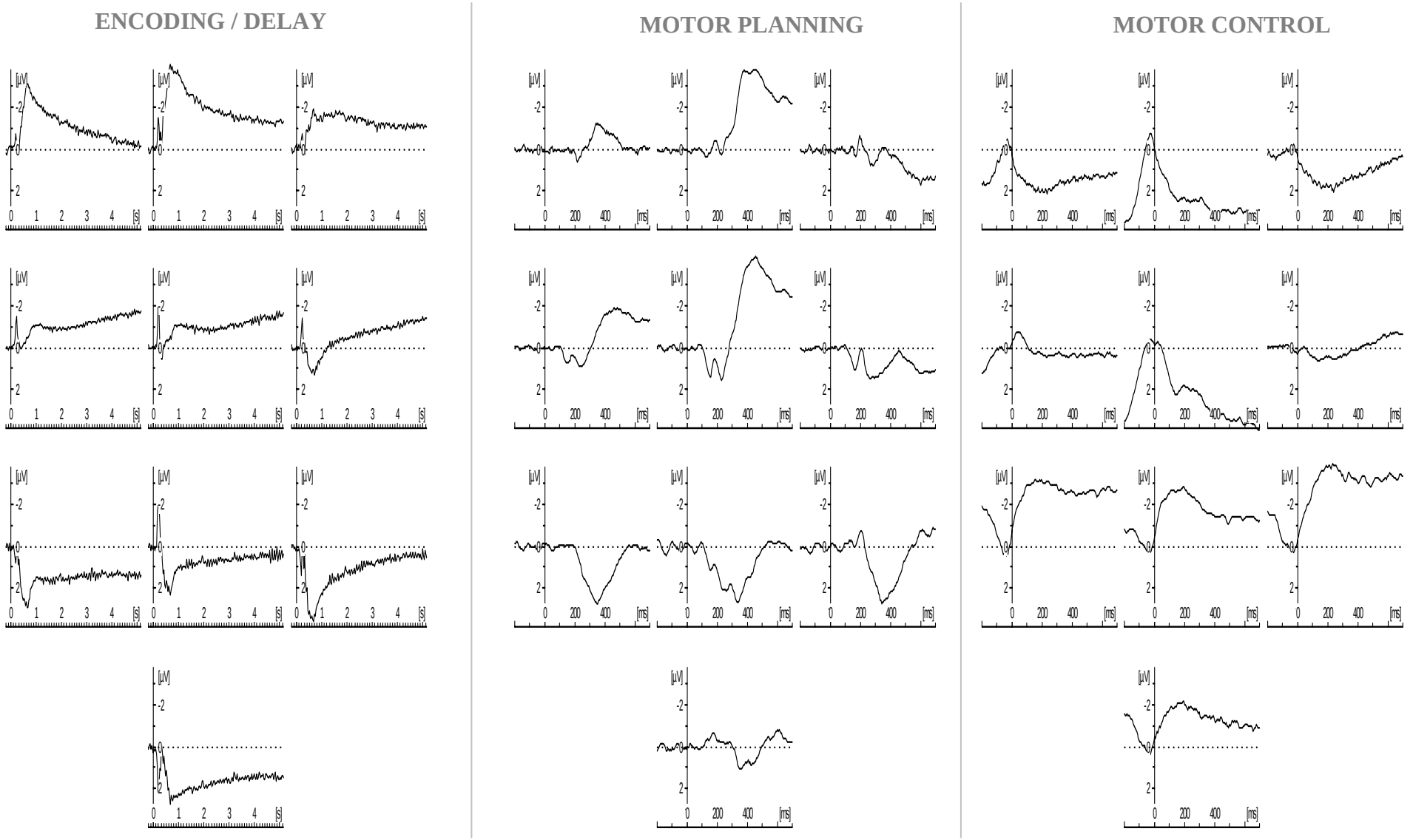


Appendix 4-B. *EEG-Study 2:* ERPs at F5, FZ, F7 (upper array), C3,CZ,C4 (second array), P3, PZ, P4 (third array) and OZ (bottom array) during the defined processing phases in the middle delay condition ("1000"). Note: all ERPs are adjusted to the respective trigger and are baseline corrected in respect to the time range of –100-0 preceding each phase.

ENCODING / DELAY | **MOTOR PLANNING** | **MOTOR CONTROL**



Appendix 4-C. *EEG-Study 2:* ERPs at F5, FZ, F7 (upper array), C3,CZ, C4 (second array), P3, PZ, P4 (third array) and OZ (bottom array) during the defined processing phases in the long delay condition ("5000"). Note: all ERPs are adjusted to the respective trigger and are baseline corrected in respect to the time range of –100-0 preceding each phase.



7 Zusammenfassung

Den Inhalt der vorliegenden Arbeit bilden die Untersuchungen der Verhaltens- und EEG-Indikatoren sensomotorischer Interaktionsprozesse in der kinästhetischen und der visuellen Modalität. Als theoretische und empirische Grundlage für die Planung der durchgeführten Experimente und für die Interpretation der Ergebnisse diente zum Einen eine Reihe von Ansätzen, die die Existenz zweier unabhängiger sensomotorischer Verarbeitungsmodi nahe legen. Dabei handelt es sich im Wesentlichen um eine Differenzierung der Art, wie sensorische Informationen für die Planung von motorischen Aktivitäten genutzt werden. Innerhalb dieses Forschungsbereichs wird es angenommen, dass bestimmte und für eine Reaktion notwendige Reizeigenschaften direkt in die motorische Planung eingehen können. Dieser Art der Verarbeitung wird ein anderer Modus gegenübergestellt, der mit Gruppierungs-, Kategorisierungs- und anderen mit Gedächtnismechanismen verbundenen Prozessen assoziiert wird. Zum Anderen flossen die Ergebnisse aus zwei weiteren relevanten Forschungsbereichen in die experimentelle Planung und die Einordnung von Ergebnissen ein. In den Untersuchungen zum motorischen bzw. kinästhetischen Gedächtnis erwiesen sich mehrere Informationsquellen, wie dynamische Bewegungsinformationen, Endstellung der Hand oder die räumliche Position des Zielobjektes als relevant für den Abruf und somit für die Planungsprozesse. In den Studien, die sich mit visuomotorischen Prozessen befassen, werden v.a. zwei Planungsschemata diskutiert. Eine Reihe von Befunden legt die Annahme nahe, dass die initialen retinazentrierten Reizinformationen einer Kaskade von Transformationsprozessen unterliegen, im Laufe derer eine räumliche Position des externalen Inputs in einem körperzentrierten Referenzsystem berechnet und mit der jeweiligen Startposition der Hand verglichen wird. Andererseits werden Ergebnisse berichtet, die eine direkte Koppelung zwischen der Reiz- und der Handposition auf der Ebene der augenzentrierten Koordinaten nahe legen.

Diese komplexe Thematik sei an einem alltäglichen Beispiel veranschaulicht. Man stellt beim Lesen einer Zeitung eine Tasse Kaffee auf den Tisch, nach der man nach einiger Zeit erneut greift. Wenn die erste Bewegung visuell nicht wahrgenommen wurde, hat das Gehirn mehrere Möglichkeiten, um eine weitere Handbewegung zu planen: es kann die dynamischen Informationen der ersten Bewegung nutzen (d.h. in diesem Fall wird die erste Bewegung erneut ausgeführt), es kann aber auch lediglich die Endstellung der Hand beim Abstellen der Tasse behalten oder eine Raumposition der Tasse relativ zu einem Referenzpunkt aus anfänglichen somatosensorischen Informationen ableiten and daraufhin die Bewegung

programmieren. Wenn visuelle Informationen vorhanden sind, kann die motorische Planung in visuellen Koordinaten erfolgen (d.h. initialle Handposition und die Position des Tasse wird auf der Ebene der initialen Verarbeitungsstufe miteinander verrechnet). Alternativ bestehet die Möglichkeit, die anfänglichen retinalen Koordinaten des Objektes bei Verwendung von Positionssignalen der Augen und des Kopfes in Köperkoordinaten umzurechnen (d.h. die Position der Tasse auf der Retina wird in die Position der Tasse relativ zu einem Körperteil, wie der Schulter transformiert). Werden die so erzeugten Zielinformationen mit der aktuellen Handstellung verglichen, resultiert ein Differenzvektor, der in die entsprechenden muskulären Kontraktionen übersetzt werden kann.

Obwohl die Existenz der zuletzt erwähnten Informationsquellen und Planungsmechanismen empirisch relativ gut belegt zu sein scheint, ist es weitgehend unbekannt, welche Faktoren die eine oder andere Art der Verarbeitung wesentlich begünstigen.

Basierend auf Befunden, die für zeitabhängige Veränderungen sensomotorischer Interaktionsmechanismen sprechen, wurden sieben Experimente durchgeführt, in denen v.a. der Einfluss der Zeit zwischen Reiz und motorischer Reaktion im Mittelpunkt des Interesses stand. Die wesentliche Frage, die es zu beantworten galt, bestand darin, ob sich Hinweise auf zeitabhängige Veränderungen sensomotorischer Prozesse feststellen lassen, und wenn ja, welchen Bezug sie zu den erwähnten Hypothesen aufweisen.

Dabei wurde auf ein Paradigma eindimensionaler linearer Bewegungen zugegriffen, das im Kontext der Studien zum motorischen Gedächtnis eingesetzt wurde. Mit Ausnahme des zweiten EEG-Experiments bestand die generelle Versuchsanordnung darin, einen leicht beweglichen Hebel, der auf der horizontalen Ebene in einer Schiene montiert war und an verschiedenen Positionen mechanisch gestoppt werden konnte, zu bewegen. Nach einem ersten imperativem Signal führten die Versuchspersonen eine Handbewegung von der Startposition aus (ca. 10 cm vor dem Körper) nach vorn auf der Ebene der Körpermittellachse. Diese wurde an einer bestimmten Position gestoppt. Anschließend musste die Hand in die Startposition zurückgeführt werden. Nach einem weiteren auditiven Signal hatten die Probanden die Aufgabe, die jeweilige Endposition der ersten Bewegung (oder die zurückgelegte Distanz im Experiment 3: *„Position vs. distance“*) mittels einer weiteren Handbewegung zu reproduzieren. Die Sicht der Apparatur wurde sowohl vor als auch während der Untersuchungen verhindert.

In den ersten zwei Experimenten wurde der Einfluss einer verbal-kognitiven und einer motorischen Aufgabe auf das Behalten kinästhetischer Informationen untersucht. Das primäre Ziel war es, mögliche Veränderungen dieser Effekte in Abhängigkeit von der Dauer des

Verzögerungsintervalls festzustellen. Dabei wurde ein ähnlicher Einfluss der implementierten Distraktor-Aufgaben erwartet, wenn Behalte- und / oder motorische Planungsprozesse innerhalb eines einheitlichen funktionales Systems stattfinden. Sollten die Interferenzeffekte sich als zeitabhängig erweisen, würde dies für Veränderungen der Verarbeitungscharakteristika sprechen.

Während des ersten Experiments (*„Mental distraction“)* mussten die Versuchspersonen nach einer ausgeführten Handbewegung und vor der Reproduktion dieser Bewegung ein Urteil über die zurückgelegte Distanz abgeben (d.h. die Entfernung in cm schätzen). In einer weiteren Bedingung wurde das Urteil nicht verlangt. Außerdem wurde das Behalteintervall manipuliert: einer unmittelbaren Reproduktion (~ 0 Sekunden) wurde eine verzögerte (~ 8 Sekunden) gegenübergestellt.

Die Wirkung der Distanzschätzung war abhängig von der Dauer des Verzögerungsintervalls: das implementierte Urteil war mit einer Verschlechterung der Leistung verbunden (d.h. mit einer höheren Variabilität der Reaktionen), wenn das Behalteintervall lang war und mit einem entgegengesetzten Trend im Falle der unmittelbaren Wiedergabe. Außerdem waren die berichteten Entfernungen sowie deren systematische Fehler von den motorisch reproduzierten Distanzen und deren Fehlern statistisch unabhängig (die entsprechenden Korrelationskoeffizienten waren sehr gering und nicht signifikant). Diese Ergebnisse deuteten darauf hin, dass die Informationen, die in die Planung der Reproduktionsbewegung eingingen, sich von denen unterschieden, die für das verbale Urteil genutzt wurden. Andererseits sprachen die Ergebnisse der Endpunktvariabilität dafür, dass Interferenzprozesse auf einer „höheren“ Verarbeitungsebene auftraten (z.B. auf dem Ebene der Aufmerksamkeitskapazität), allerdings nur, wenn die Reproduktion verzögert wurde. Dies konnte als ein Hinweis für zeitabhängige Veränderungen der Verarbeitungscharakteristika gedeutet werden.

Im zweiten Experiment (*„Motor distraction“)* folgte nach der ersten Bewegung und vor der Reproduktion eine „Zwischenbewegung“ mit der rechten vs. linken Hand, deren Einfluss weitere Hinweise über die Art der Informationen liefern sollte, auf deren Grundlage die Reproduktionsbewegung programmiert wird. Die Versuchspersonen wurden angewiesen, eine kurze Bewegung von etwa 10 cm sofort nach dem Ende der ersten Rückbewegung („unmittelbare Reproduktion“) oder nach einem zusätzlichen akustischen Signal, das ca. 4 Sekunden nach dem Ende der Rückbewegung erfolgte („verzögerte Reproduktion“) auszuführen. Die Manipulation des Verzögerungsintervalls entsprach der des ersten Experiments („0“ vs. „8“ Sekunden).

Der systematische Fehler („Konstanter Fehler“) variierte in Abhängigkeit davon, wann die jeweilige Zwischenbewegung ausgeführt wurde bzw. wann die Reproduktion erfolgte. Das kurze Verzögerungsintervall war mit einer stärkeren Tendenz zu überschätzen assoziiert, als die Zwischenbewegung mit der linken Hand ausgeführt wurde, im Vergleich zu der Bedingung, in der nur die rechte Hand genutzt wurde. Die Verlängerung des zeitlichen Abstandes zwischen der Enkodierung und der Reproduktion äußerte sich in einer Umkehrung dieses Zusammenhangs. Allerdings erwies sich auch die Amplitude der Zwischenbewegung als sensitiv in bezug auf die Zeit- und Distraktormanipulationen. Dennoch konnte die reine Amplitudendifferenz der Zwischenbewegung die beobachteten Effekte des systematischen Fehlers nicht erklären. In Anlehnung an frühere Studien zum motorischen Gedächtnis und aktuelle Befunde zur Hirnasymmetrie im motorischen Kontext, deuteten die Ergebnisse darauf hin, dass die durch die Zwischenbewegungen induzierten Interferenzprozesse unterschiedliche Repräsentationen in Abhängigkeit von dem Effektor und der Zeit der Reproduktion umfassten.

Insgesamt legten die Ergebnisse der ersten beiden Experimente die Schlussfolgerung nahe, dass eine unmittelbare Reproduktion mit einem Zugriff auf eher dynamische Bewegungsinformationen einherging. Im Gegensatz dazu, schien eine verzögerte Widergabe mit statischen Aspekten, wie der Endstellung der Hand oder räumlichen Position des Reizes assoziiert zu sein.

Darauf aufbauend wurde eine weitere Studie (*„Position vs. distance“)* durchgeführt, im Rahmen derer, die Merkmale dynamischer und statischer Information eingegrenzt and ihre mögliche Zeitabhängigkeit geprüft werden sollte.

Die Ursprüngliche Versuchsanordnung wurde insofern modifiziert, als die Anzahl der mechanischen Sperrvorrichtungen, die die unterschiedlichen Bewegungsdistanzen definierten, von 8 auf 6 reduziert wurde. Außerdem wurde jetzt die erste Rückbewegung vor der initialen Startposition gestoppt (ca. 9 cm davor). Die Aufgabe der Versuchspersonen bestand darin, von diesem neuen Startpunkt aus entweder die zurückgelegte Distanz oder die Position des „Targets“ (sprich die Position, an der die erste Bewegung gestoppt wurde) zu reproduzieren. Das Verzögerungsintervalls wurde in der gleichen Weise manipuliert, wie in den Experimenten zuvor („0“ vs. „8“ Sekunden).

Beide Reproduktionsbedingungen („Distanz“ und „Position“) waren mit einem jeweiligen charakteristischen Muster kinematischer Parametern begleitet. Während die Reproduktion der Endpositionen im Wesentlichen üblichen distanzspezifischen Veränderungen entsprach, die auch bei Bewegungen zu visuellen Reizen zu beobachten sind, war die Distanz-Reproduktion

mit einer eher untypischen Strategie der Bewegungsteuerung assoziiert, was sich v.a. in der Anpassung der Beschleunigung an die unterschiedliche Länge der Bewegung niederschlug. Im Falle der Positionsreproduktion führte der Anstieg der Bewegungsdistanz zu einer „Erhöhung“ der maximalen und der minimalen Beschleunigung. Im Gegensatz dazu stieg die maximale Beschleunigung mit wachsender Distanz nur geringfügig an, während die minimale Beschleunigung einen deutlichen Trend in Richtung der Intensitätsabnahme aufwies, als die Probanden die zurückgelegte Distanz reproduzierten.

Diese unterschiedlichen Muster ließen sich z.T. auf die Kinematik der ersten Bewegung zurückführen. Die maximalen Beschleunigungsamplituden differenzierten nicht nach Bewegungsdistanz und die minimalen Amplituden sanken mit zunehmender Entfernung. Dieses Ergebnis ließ sich im Kontext der gegebenen Versuchsanordnung verstehen. Da die Probanden nicht wussten, an welcher Stelle die Bewegung gestoppt wird, waren sie darauf angewiesen eine „Default-Trajektorie“ auszuwählen, die sehr wahrscheinlich auf eine „weite“ Entfernung gerichtet war (da die Beschleunigungstrajektorie mit wachsender Entfernung immer „natürlicher“ wurde). Die untypische Form des Beschleunigungsverlaufs, die während der Reproduktionsphase bei der Distanzwiedergabe beobachtet wurde, schien demzufolge der Beschleunigungstrajektorie der Enkodierungsphase zu ähneln. In Anlehnung darauf, lag die Schlussfolgerung nahe, dass während der Distanzreproduktion v.a. die dynamischen Informationen der ersten Bewegung in die Planung der Reproduktionsbewegung eingingen, während im Falle der Positionsreproduktion man eher einer Quelle, wie der räumlichen Position des Reizes folgte. Diese Hypothese schien auch bestätigt durch die durchgeführte Korrelationsanalyse, die einen stärkeren Zusammenhang zwischen der Bewegungsdistanz und der Amplitude der maximalen Beschleunigung bei der Reproduktion von Positionen vergleichen mit der Distanzwiedergabe und einem umgekehrten Zusammenhang bei den Korrelationen zwischen der maximalen Beschleunigung und der Dauer der Bewegung nahe legte.

Die Ergebnisse des letzten Experiments lagen den Schluss nahe, dass die Nutzung von dynamischen und statischen Informationsquellen unter gegebenen Versuchsbedingungen sich v.a. in der minimalen Beschleunigung äußerte. Darauf aufbauend wurden zwei weitere Experimente durchgeführt, die mögliche Veränderungen dieses Parameters sowie den Verlauf von systematischen und variablen Fehlern im Bereich von Millisekunden und Sekunden erfassen sollten.

Im vierten Experiment („*Forgetting in the milliseconds range*“) wurde das Interstimulusintervall so angepasst, dass das imperative Signal für die Reproduktion

annähernd 0, 200, 400, 600 und 800ms nach dem Ende der ersten Rückbewegung erfolgte. Die Probanden hatten die Aufgabe, die Endposition der ersten Bewegung zu reproduzieren. Es wurden keine weiteren Restriktionen, wie eine Startveränderung oder zusätzliche Aufgaben implementiert. Ein wesentliches Ergebnis in bezug auf die Beschleunigung während der Reproduktionsphase bestand darin, dass relativ unabhängig von der Zeitmanipulation eine Abnahme der Intensität mit der Zunahme der Bewegungsdistanz festgestellt wurde. Dies deutete darauf hin, dass die Probanden eine ähnliche Strategie anwandten, wie in der Distanzbedingung der vorherigen Studie. D.h. sie nutzen eher die dynamischen Informationen der ersten Bewegung für die Planung der Reproduktion, als sie sich an der statischen Raumposition und / oder finalen Handstellung orientierten.
Für das fünfte Verhaltensexperiment (*„Forgetting in the seconds range“*) wurde das methodische Vorgehen mit Ausnahme der Länge der Verzögerungsintervalle im Wesentlichen beibehalten. Die Reproduktionsbewegung erfolgte annähernd 0,1,2,4,6 und 8 Sekunden nach dem Ende der ersten Rückbewegung.
Die distanzspezifische Skalierung der minimalen Beschleunigung unter den „kurzen“ Intervall-Bedingungen (0 und 1) war vergleichbar mit dem Muster des vorherigen Experiments und der Distanzbedingung der dritten Studie, wo eine Zunahme der Bewegungsdistanz mit einer Abnahme der (negativen) Amplitude assoziiert war. Eine weitere Verlängerung des Zeitintervalls äußerte sich in einer sukzessiven Abweichung von dieser untypischen Modulation und einer Veränderung in Richtung der Positionsbedingung der vorherigen Studie. Außerdem konnten wir feststellen, dass ein „Effekt der zentralen Tendenz“ (die Tendenz, geringe Distanzen zu überschätzen und weite Entfernungen zu unterschätzen) ab etwa 2 Sekunden auftrat, der im Millisekundenbereich nicht vorhanden war. Dies deutete darauf hin, dass der Einfluss des Kontextes (Bereich der Positionen) auf die Reproduktion erst ab einem Intervall von ca. 2 Sekunden auftrat, während davor man hauptsächlich der sensorischen Spur der ersten Bewegung folgte.
Die skizzierten Ergebnisse der ersten fünf Experimente schienen die Annahme zu bestätigen, dass in Abhängigkeit von dem Zeitpunkt der Reaktion unterschiedliche Informationsquellen in die motorische Planung involviert sein können. Diese Veränderungen könnten mit der anfangs erwähnten Dimensionen der sensomotorischen Verarbeitung im Zusammenhag stehen. Allerdings, konnten wir auch Ansatzpunkte finden, die mit den „Dual-System-Annahmen“ sowie den erwähnten Planungsschemata nicht vollständig vereinbar waren.
Im Rahmen der ersten EEG Studie (*EEG-Study 1*) sollte der Frage nachgegangen werden, wie eine Verzögerung der Reaktion sich auf die hirnelektrischen Indikatoren von Behalte-,

Planung- und Steuerungsmechanismen auswirkt. In Ahnlehnung an die Ergebnisse aus den Verhaltensstudien erwarteten wir Unterschiede in der Modulation der Aktivität in den entsprechenden Verarbeitungsphasen, die einen Aufschluss über die dynamischen und regionalen Aspekte der beteiligten Mechanismen liefern sollten.
Die Aufgabe der Versuchspersonen war die gleiche, wie in den letzten zwei Experimenten. Nach einem ersten imperativen Signal wurde eine Handbewegung ausgeführt, die an einer bestimmten Position mechanisch gestoppt und nach einer Verzögerung reproduziert wurde. Die Zeit wurde so manipuliert, dass das imperative Signal für die Reproduktion im Bereich von zwei hundert Millisekunden („0“), einer Sekunde („1“) und fünf Sekunden („5“) erfolgte. Neben Verhaltensdaten wurde die evozierte EEG Aktivität in bezug auf die implementierten Manipulationen in mehreren definierten Verarbeitungsepochen analysiert.
Die Analyse der Verhaltensdaten erbrach zusätzliche Hinweise darauf, dass der Einfluss der Reaktionsverzögerung sich v.a. in einer Verschiebung der Dominanz von eher dynamischen zu eher statischen Kontrollmechanismen äußerte. In der kurzen Zeit-Bedingung („0“) war die maximale Beschleunigung während der Reproduktionsbewegung in allen Distanzbedingungen vergleichbar (sowie im Falle der Enkodierungsbewegung). Die Verlängerung des Verzögerungsintervalls führte zu einer sukzessiven Reduktion dieses Kennwertes mit der Abnahme der Bewegungsdistanz, wenn man die Werte der ersten Bewegung als Referenz betrachtete. Dieses Ergebnis lieferte Hinweise darauf, dass der initiale „Kraftimpuls“ für die nahen Distanzen zu hoch war und im Falle der unmittelbaren Reproduktion nicht korrigiert wurde. D.h. eine Differenzierung der Geschwindigkeiten und der Bewegungsdistanzen wurde hier v.a. durch die Modulation der zeitlichen Aspekte der Bewegungssteuerung erreicht (z.B. durch eine Verkürzung der Beschleunigungsdauer bei nahen Positionen). Diese unterschiedlichen Strategien der frühen Bewegungssteuerung, die man in Verbindung mit der Anpassung von „Puls-Breite“ („pulse-width“) und „Puls-Höhe“ („pulse-height“) bringt, wurden auch im EEG in Form einer unterschiedlichen intervall- und distanzspezifischen Modulation einer negativen Komponente („MP“, „motor potential“) unmittelbar vor dem und einer positiven Komponente („P2“) nach dem Beginn der Reproduktionsbewegung sichtbar. Korrelierte man die maximale Amplitude der Beschleunigung mit der Distanz und der Dauer der Enkodierungs- und Reproduktionsbewegungen, so ließ sich eine Veränderung der Zusammenhänge feststellen, die in Richtung eines Anstieges von „statischen“ (max. Beschl. & Distanz) und einer Abnahme von „dynamischen“ Korrelationen (max. Beschl. & Dauer) mit wachsendem Verzögerungsintervall erfolgte.

Außerdem konnten wir feststellen, dass die EKP Amplitude in mehreren Verarbeitungsepochen, angefangen mit dem Ende der ersten Rückbewegung, durch die Zeit Manipulation moduliert wurde. Ein charakteristisches Merkmal dieser Unterschiede schien v.a. in einer Asymmetrie der Aktivation zu bestehen. Betrachtete man z.B. die späte Phase des Behalteintervalls, so war die Amplitude negativer EKPs über den premotorischen Regionen der linken Hemisphäre im Falle der kurzen Zeit-Bedingung („0“) höher, als über den homologen Arealen der rechten Hemisphäre. In der mittleren Bedingung („1“) war dieser Unterschied reduziert. Wurde die Reproduktion erst nach 5 Sekunden verlangt, war die rechte Hemisphäre stärker aktiviert als die linke. Ein ähnlicher Zusammenhang wurde beobachtet, als die Endphase der Bewegungssteuerung analysiert wurde. Diese Ergebnisse schienen im Einklang mit den Verhaltensdaten sowie mit Befunden zur Hirnasymmetrie im Kontext motorischer Forschung zu stehen. Eine aktuelle Hypothese geht davon aus, dass die linke Hemisphäre in die Verarbeitung von v.a. dynamischen Aspekten einer Bewegung involviert ist (z.B. in die Kontrolle der Trajektorie), während die rechte v.a. statische Aspekte, wie die Endstellung und/oder die Endposition steuert.

Insgesamt ergaben die EEG Daten ein komplexes Bild. So konnten wir Hinweise finden, die für die Beteiligung von qualitativ unterschiedlichen frontoparietalen Netzwerken in Abhängigkeit von dem Zeitpunkt der Reproduktion sprachen. Diese, sowie weitere Ergebnisse deuteten auf eine dreifache Dissoziation funktionaler Mechanismen hin, die je nach Zeitpunkt des Abrufs involviert sein können.

Die zweite EEG Studie (*EEG-Study 2*) sollte der Frage nachgehen, ob ähnliche Zusammenhänge sich auch in der visuellen Modalität feststellen lassen. Die Probanden fixierten eine Leuchtdiode, die auf der Höhe der Augenposition in ca. 1 Meter Abstand platziert war. Die bisher benutzte Apparatur wurde insoweit modifiziert, als anstatt mechanischer Sperrvorrichtungen, LEDs eingebaut wurden. Nach einem Warnton leuchtete ein von den acht verwendeten Reizen (LEDs) für 50 ms auf, die das jeweilige Bewegungsziel repräsentierten. Nach dem Erlöschen des Fixationslichtes, dass 200, 1000 und 5000 ms nach dem Reizoffset erfolgte, hatten die Probanden die Aufgabe eine Handbewegung zu dem jeweiligen Ziel auszuführen.

Die Analyse der EKPs der Planungsphase ergab wesentliche Unterschiede in der evozierten Aktivität in Abhängigkeit von der Länge des Verzögerungsintervalls. Während eine negative Komponente an den frontozentralen Elektrodenpositionen in allen drei Bedingungen vergleichbar war („MP“), zeigten sich v.a. an den posterioren Positionen deutliche Unterschiede. Charakteristisch für die kurze Zeit-Bedingung war die „evozierte alpha

Aktivität“, die v.a. die okzipitalen Elektroden umfasste. Vor der Ausbildung des MP war in der mittleren Bedingung („1“) eine negative phasische Komponente über den temporookzipitalen Regionen festzustellen. Diese war ebenfalls vorhanden, wenn die Reaktion erst nach 5 Sekunden erfolgte. Allerdings, deutete eine Abfolge von weiteren Potentialen, die zeitlich zwischen der letzteren und dem MP angeordnet waren auf einen zusätzlichen Prozess hin, der in den kürzeren Zeitbedingungen nicht vorhanden zu sein schien. Außerdem traten die Distanzunterschiede unmittelbar vor dem Begin der Reproduktionsbewegung an unterschiedlichen Elektroden in Abhängigkeit von der Länge des Verzögerungsintervalls auf. Diese Ergebnisse waren am ehesten vereinbar mit der Annahme unterschiedlicher Aufrechterhaltemechanismen, die in Anlehnung an die Literatur mit einem „sensorischen“, einen „perzeptuellen“ und einem „Kurzzeitgedächtnis“ im Zusammenhang stehen könnten.

Weiterhin konnten wir in beiden EEG-Experimenten eine distanzspezifische Modulation einer Reihe von EKP-Komponenten beobachten, die unmittelbar vor bzw. nach dem Bewegungsbeginn auftrat. Die temporalen und regionalen Eigenschaften dieser Aktivierungsmuster wurden in Verbindung mit möglichen funktionalen Aspekten der Programmierung und der Bewegungssteuerung gebracht. Insbesondere eine ab ca. 130ms nach dem Beginn der Bewegung auftretende Negativierung über den primären motorischen Arealen deutete auf einen wichtigen Prozess hin, der neue Erkenntnisse in bezug auf die neuronalen Mechanismen der Kontrolle von schnellen ballistischen Bewegungen nahe legte. In Anlehnung an eine Korrelationsanalyse, schien das Ergebnis die Annahme zu bestätigen, dass es sich dabei um ein Mechanismus der Trajektorienanpassung handele, der von der Distanz und der Dauer der Bewegung abhängig ist.

Zusammenfassend lasst sich feststellen, dass die angenommene Dichotomie der sensomotorischen Verarbeitung sowie das zugeschriebene neuronale Substrat möglicherweise eine Übervereinfachung darstellen. Obwohl die Ergebnisse der durchgeführten Studien im Kern diesen Ansätzen sowie den erwähnten Planungsschemata nicht zu widersprechen scheinen, legen sie ein komplexeres und dynamisches Bild nahe, bei dem die Sensorik und die Motorik auf unterschiedlichen hierarchischen Verarbeitungsebenen gekoppelt werden können.

8 Erklärung

Ich versichere, dass ich meine Dissertation

**„From stimulus to response:
Analyses of electrophysiological and behavioral indicators of sensorimotor interaction processes in linear movements to kinesthetically and visually defined spatial locations"**

selbständig und ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

_____ _____

(Ort/Datum) (Unterschrift mit Vor- und Zuname)